

The Development of the Heart and Vascular System of *Lepidosiren paradoxa*.

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With Plate 5 and 31 Text-figs.

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I. INTRODUCTION.

In the following account of the development of the heart and blood-vessels of *Lepidosiren paradoxa* I have endeavoured to trace their main morphological rather than their minute anatomical relations. I trust that few points of importance have been neglected, though probably many minutiae of interest have been passed over.

The account of the adult condition has been obtained partly from the dissection of one complete and one bisected individual (cranial half), whose vessels were injected with a gelatine mass at air temperature on a hot tropical afternoon (the vessels were first washed out with normal saline solution, nitrite of amyl being administered to keep the arterioles dilated), and partly from the dissection of a dozen uninjected adult heads, which included the cardiac region and heart. This account only includes the more obvious details that could be ascertained by a conservative dissection of the injected material mentioned. The account of the development of the vascular system has been obtained from the scrutiny of serial sections in three planes of a complete series of embryos from Stage 23—when the vessel rudiments first appear—to Stage 38, when the adult condition in all but size has been attained. The finer morphological and anatomical relations of the adult, therefore, have been noted in conjunction with the examination of the development of the various parts of the vascular system, Stage 38 of the sectional material being considered as equivalent to the adult condition. The portal system, it will be noticed, is reported only in the notes on the development of the venous system, as it was considered unnecessary to submit the valuable injected specimens to the serious disturbance involved by the dissection of the vessels of that system. The study of the development of the heart was further facilitated by the dissection under the Zeiss binocular dissecting microscope of embryos of varying ages.

Throughout these notes I have called the distal arterial segment of the heart the *bulbus cordis*. I am aware that it is still a matter of debate whether this region of the heart is more correctly entitled *conus* (8) or *bulbus*, but meantime, till a final solution of the question is reached, I have preferred to employ a nomenclature that brings this account more easily into line with the work of Langer (16) and Greil (9).

I have to express my great indebtedness to Professor Graham Kerr for free access to all his valuable *Lepidosiren*

material and for much helpful criticism throughout the course of my work.

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II. SUMMARY OF GENERAL FEATURES OF THE VASCULAR SYSTEM OF LEPIDOSIREN.

The main points of interest in the comparative anatomy of the heart and vascular system of *Lepidosiren* are here briefly summarised. Further references will be found in the text in the course of the article itself.

The heart of *Lepidosiren* is distinguished by the presence of well-marked, though incomplete, auricular, ventricular and bulbar septa, the absence of any pocket or semilunar valves, and the separate opening of the pulmonary vein into the left auricle. Two other distinctive features are the long, abruptly curved bulbus cordis, and the single button-like plug that acts as an auriculo-ventricular valve. The heart of *Lepidosiren* most closely resembles that of *Protopterus* (2), but differs from it in possessing definite, though incomplete, interauricular and interventricular septa. Compared with the heart of *Ceratodus* (2) and (14), the main points of difference are: (1) The more abrupt kinking of the bulbus cordis; (2) the almost complete disappearance in *Lepidosiren* of all the bulbar pocket valves as such, except proximally, where a few vestigial valves still persist (17); (3) the development of the spiral valve as a structure that extends throughout the length of the bulbus; (4) the presence of a longitudinal valve on the left wall of the distal part of the bulbus; (5) the shortening of the posterior auricular wall, so that in *Lepidosiren* the sinu-auricular and auriculo-ventricular openings are closely approximated. In *Lepidosiren* the ventricle is comparatively a larger part of the heart, and the interventricular septum is much more definitely a septal structure, though its attachments appear to be identical;

while the auriculo-ventricular plug or fibro-cartilage is apparently better adapted for closing the auriculo-ventricular opening than the similar structure in the heart of *Ceratodus*. In short, the heart of *Lepidosiren*, as compared with that of *Ceratodus*, shows a marked advance in the development of a mechanism for the more complete separation of the arterial and venous blood-streams.

The general facts of the development of the heart are comparable with those described for the Elasmobranchs (12) in so far as the division into different chambers is concerned; the details, however, differ considerably. In *Lepidosiren* the auricular canal is only transitorily a distinct external division of the heart, and early loses its identity in the auriculo-ventricular opening. The posterior auricular wall remains very short and the sinu-auricular and auriculo-ventricular openings are consequently close together. The auriculo-ventricular plug, which is apparently a peculiarly dipnoan structure and which seems to be identically developed in *Ceratodus* (14), can, however, be compared in origin and function both to the posterior (dorsal) auriculo-ventricular valve of the Elasmobranchs, and to the posterior (dorsal) sinu-auricular valve in *Lepidosteus* (2), but at no period is there any equivalent to an anterior (ventral) valve. The right sinu-auricular valve develops as the similar structure in the Elasmobranchs, but it is often very poorly developed and there is no left valve. The pulmonary vein develops in the left wall and roof of the sinus venosus, and opens, from the first, directly into the left auricle as in the reptilian heart (21), the auricular connection of this vein in the Urodele being a secondary, not a primary condition. The interauricular septum of *Lepidosiren* develops in the same way as that of the Urodeles (12), except that the termination of the pulmonary vein projects somewhat into the auricles in the former, and actually forms the most posterior part of the septum. The development of muscular trabeculæ in the ventricle proceeds as in all the Vertebrata; similarly they extend into the auricular canal and become continuous with

the valvular apparatus, the auriculo-ventricular plug, situated there. This structure, however, with its thick, centrally placed muscular attachment on its ventral surface, does not become hollowed out to form a pocket valve, but gives rise to the typically dipnoan auriculo-ventricular plug. The development of the long bulbus cordis resembles in some degree that of the same division of the heart in the Elasmobranchs, e.g. in the appearance for a time during development of four endocardial cushions in the distal and proximal parts of the bulbus, and the persistence proximally in the adult of three rows of vestigial pocket valves, as well as of transverse furrows at the base of the spiral valve. The discontinuous development of the spiral valve in two segments can be compared with the similar condition in Urodeles (16). The heart of *Lepidosiren* therefore presents different elasmobranch, amphibian, and even reptilian, as well as some peculiarly dipnoan characters.

Some of the main points of interest in the arterial system are the development of six aortic arches, and the close resemblance of their ultimate arrangement to that present in the Urodeles (3), the lingual and dorsal carotid arteries of *Lepidosiren* corresponding to the external and internal carotids of the former. The pulmonary arteries are developed directly in connection with the sixth aortic arches, and come to open secondarily from the dorsal aortic roots; whereas in the urodele they are tending to become more direct continuations of the sixth aortic vessels. The development of the cœliac artery as primarily the right glomerular vessel is comparable with the teleostean condition, but its lack of further connections with any other vessels except in the wall of the gut appears to be a detail peculiar to *Lepidosiren*.

In the venous system the development of the anterior cardinal veins tallies generally with that of the Elasmobranchs and amphibians, while that of the posterior cardinal veins agrees with the amphibian type, except that in *Lepidosiren* the fused interrenal portions of the two vessels become separated again. The anterior section of the posterior vena

cava develops centripetally towards the heart, and is to be looked on as a short cut connecting the large right posterior cardinal vein with the heart. Both posterior cardinals persist in the adult, the left in its entirety, the right only as a comparatively short vessel. The development of the sub-intestinal and portal veins is essentially Elasmobranch (20) in character.

The vascular system of *Lepidosiren* would thus appear to have many points in common with both the Elasmobranchs and the amphibians, and to occupy a position between the two, though tending more towards the latter. As was to be expected, the adult conditions are almost identical with those described for *Protopterus*; some of the main points agree with those given for *Ceratodus*, but the details of the vascular system of the latter—apart from the heart—appear to be much more closely piscine than in *Lepidosiren*.

THE HEART AND VASCULAR SYSTEM OF THE ADULT LEPIDOSIREN.

(A) Heart.

In *Lepidosiren* the heart is placed far forward and lies in a thick pericardiac envelope that splits into two layers in the lateral and ventral portions of its posterior half. This split forms a lymph space over the posterior part of the ventral surface of the inner pericardium; the two pericardiac layers come together again at the entrance of the posterior vena cava into the sinus venosus. The pericardium is attached to the heart over the dorsal surface of the sinus venosus, round the posterior vena cava as it enters the sinus, to the ventral surface of the ventricle by a special fibrous band—*gubernaculum cordis* of Fritsch (7)—and to the anterior extremity of the bulbus cordis. The outer surface of the pericardium is firmly attached at the sides to the body musculature and anteriorly to the pectoral girdle.

The heart as a whole is of irregular oval shape (Pl. 5, figs.

1 and 2) measuring in one large adult male $2\frac{1}{4}$ by 1 in. ; the ventricle forms little more than half the length, the rest being due to the bulbus cordis. The heart is fixed in the pericardiac cavity as described above ; it is almost mesial in position, and the apex is directed backwards, a little ventrally and to the left. The heart is wrapped in a fine sheath of lymphatics, which invests the ventricles and auricles closely, but is looser and more prominent over the bulbus and in the grooves between the different cardiac compartments, the auricles in fact are held applied to the posterior and lateral surfaces of the bulbus by this sheathing.

Sinus Venosus.—The sinus venosus is a comparatively large, thin-walled compartment of irregular pear shape, situated posteriorly on the dorsal surface, and to the right side of the heart (Pl. 5, figs. 1 and 2, *S. V.*). It is demarcated from the auricles by a groove, especially well marked on the right side, which is the external expression of a fold guarding the sinu-auricular aperture (Pl. 5, fig. 1, *r. S. A.*) ; the roof or dorsal wall of the sinus is continuous with the pericardium (Pl. 5, figs. 1 and 2, *Per.*) and the pulmonary vein (Pl. 5, fig. 1, *P. V.*) crosses it from right to left; posteriorly, the posterior vena cava (Pl. 5, fig. 1, *P. V. C.*) opens into the sinus and in front of this the little coronary vein (Pl. 5, fig. 1, *C. V.*) from the dorsal wall of the right ventricle opens on its floor. The ventral wall of the sinus rests upon the dorsal wall of the ventricles posteriorly and upon that of the auricles anteriorly where the two ducts of Cuvier open into it (Pl. 5, fig. 1, *r. D. C.* and *l. D. C.*). The apertures of these vessels are separated from one another by the posterior border of a fold projecting obliquely from the roof and anterior wall of the sinus and which contains the pulmonary vein. This oblique fold divides the anterior part of the sinus somewhat unequally into a smaller left and a larger right compartment : the right compartment receives in front the right ductus Cuvieri, whilst below this, to the right of the oblique fold, is the sinu-auri-

cular orifice (Pl. 5, fig. 1); the left compartment receives in front the left ductus Cuvieri.

The sinu-auricular aperture (Pl. 5, fig. 1) is comparatively large and oval in shape and opens into the right auricle immediately to the right of the pulmonary fold (Pl. 5, fig. 1, *p. f.*). The opening is guarded on its right side by the vertical fold already mentioned that projects from the region of the sinu-auricular groove (Pl. 5, fig. 1, *r. S. A.*); the degree of development of this fold, however, varies very much in different specimens; in one it was represented merely by irregular thickened projections of the right rim of the sinu-auricular opening. A similar variability is noted for *Protopterus* (2), *Amia*, *Lepidosiren* and *Polypterus* (21).

Auricles.—The auricles are large, extremely thin-walled structures which, when dilated, bulge round the bulbus cordis and ventricles so as almost completely to surround them; they are markedly lobed and their margins are more or less digitate. There is no distinct external division between the two auricles, the situation of the interauricular septum being indicated only by a faint groove. The right auricle is the larger of the two; its long anterior process is wrapped round the ventral surface of the distal part of the bulbus cordis, a middle or transverse process reaches the middle line of the ventral surface of the heart at the anterior end of the ventricles, and its lower margin reaches, in some instances, to the apex. Both auricles are attached round the margins of the auriculo-ventricular aperture (Pl. 5, figs. 1 and 2), and are held applied against the bulbus by the lymphatic sheathing already described. The ventral wall of the auricle and the dorsal wall of the bulbus cordis form a sharp projecting rim internally, and a corresponding bulbo-auricular groove externally round the anterior part of the auriculo-ventricular opening (Pl. 5, figs. 1 and 2, *B.A. g.*) Dorsally and to the right the auricles are attached to the sinus venosus, but only the right auricle communicates with that compartment.

Posteriorly, projecting into and between the auricles where

they are attached to the posterior margin of the auriculo-ventricular opening, is a fold in which the pulmonary vein reaches the left auricle (Pl. 5, fig. 1, *p. f.*); this fold projects across, and is attached along the dorsal surface of, the auriculo-ventricular plug and forms the posterior part of the interauricular septum. The cavities of both auricles are traversed from roof to floor by a delicate loose meshwork of muscular bands, except in the region of the auriculo-ventricular aperture; this meshwork condenses in front of the pulmonary fold and is attached to it to complete the interauricular septum (Pl. 5, figs. 1 and 2, *A.S.* and *P. f.*). The meshwork passes from the anterior margin of the pulmonary fold to the ventral auricular wall (applied against the dorsal wall of the proximal part of the bulbus), arching across the narrow space between the margin of the auriculo-ventricular plug and the anterior rim of the auriculo-ventricular opening (Pl. 5, figs. 1 and 2).

The closeness and extent of this trabecular meshwork in the region of the auricular septum seems, however, to vary greatly in different specimens: in some the trabeculæ are numerous and compactly arranged, projecting considerably into the auricle, and there may be sheets of fine connective tissue between them, while in the others the trabeculæ are fewer and widely separate without any intervening connective tissue.

The interauricular septum, therefore, is composed of two elements which are joined together: a pulmonary fold posteriorly, and the auricular meshwork anteriorly (Pl. 5, figs. 1 and 2). This septum, however, does not ever completely shut off the two auricles from one another, there being always a space left just over the auriculo-ventricular opening.

As already noted, the pulmonary vein opens into the left auricle on the left surface of the posterior part of the interauricular septum (pulmonary fold), immediately dorsal to the left half of the auriculo-ventricular plug, and its opening is guarded by a hood-like fold that is attached ventrally to the anterior rim of the auriculo-ventricular plug (Pl. 5, fig. 2,

P. V. and *P. f.*). There are no auricular valves of any kind except the auriculo-ventricular plug.

Auricular Canal.—The auricular canal cannot be recognised as a special division of the heart, and it is represented apparently only by a narrow flattened band of musculature on the rim of the auriculo-ventricular opening converging dorsally on to the auriculo-ventricular plug. On dissection, this musculature of the auricular canal is found to be continuous anteriorly with the proximal part of the dorsal wall of the bulbus cordis, and laterally with the auricular musculature on the one hand and the ventricular on the other, round the rim of the auriculo-ventricular opening ; posteriorly it becomes continuous with the musculature of the interventricular septum at the site of attachment of the auriculo-ventricular plug to the rim of the auriculo-ventricular opening.

Ventricles.—The ventricular portion of the heart is a thick-walled muscular structure more or less enclosed between the two auricles and from which the bulbus cordis arises anteriorly (Pl. 5, figs. 1 and 2). The ventral surface of the ventricle presents no remarkable features. Near the apex there is the little fibrous band (Pl. 5, fig. 7) that binds the heart to the pericardium (this has been dissected away in Pl. 5, figs. 1 and 2). The continuity of the dorsal wall of the ventricles is interrupted by the large horse-shoe-shaped auriculo-ventricular opening that lies in the middle of the dorsal surface of the heart (Pl. 5, figs. 1 and 2). The margins of this aperture sweep round on either side to meet the conspicuous auriculo-ventricular plug posteriorly. Externally there is no indication of any division of the ventricular part of the heart into two compartments.

Attached, and immediately anterior to the posterior margin of the auriculo-ventricular opening, lying over the aperture—really in it—is a prominent, rather button-like structure of cartilaginous consistency—the auriculo-ventricular plug (Pl. 5, figs. 1 and 2, *A.V. pl.*). This structure, being in front of the posterior margin of the auriculo-ventricular opening, is enclosed by the auricular walls, and, owing to the posterior

part of the interauricular septum (pulmonary fold, Pl. 5, fig. 1, *p. f.*) being attached across the middle of its dorsal surface, the left half of that surface is enclosed in the left, the right in the right auricle; its ventral surface gives attachment to the interventricular septum (Pl. 5, figs. 1 and 2, *A. V. pl.* and *V. S.*). This plug, as stated, lies over the auriculo-ventricular aperture, and when approximated against it closes it accurately.

The interventricular septum is a thick muscular partition, whose fibres radiate fanwise from the ventral surface of the auriculo-ventricular plug to the apex and ventral and lateral walls of the ventricle, its free anterior border (round which the ventricles can communicate) passes posterior to the ventriculo-bulbar opening (Pl. 5, figs. 1 and 2, *V. S.*).

Bulbus Cordis.—The bulbus cordis is a tubular structure that arises anteriorly from the dorsal surface of the ventricles and forms a considerable portion of the heart. It presents a characteristic transverse bulging in its middle part, and its dorsal and lateral surfaces are partially concealed by the auricles; reference has already been made to its lymphatic sheathing.

The bulbus may be divided into three parts: (1) A comparatively short proximal part directed antero-posteriorly and opening from the ventricles a little anterior to the free margin of the interventricular septum (Pl. 5, figs. 1, 2 and 4, *B. C. p.*); (2) a short transverse part (demarcated externally from (1) by a distinct circular groove), directed from right to left and exhibiting a marked bulging of its ventral wall (Pl. 5, figs. 1, 2 and 4, *B. C. t.*); (3) a longer distal part, again directed antero-posteriorly (Pl. 5, figs. 1, 2 and 4, *B. C. d.*), and whose apex forms the extremely short ventral aorta from which the aortic arches take origin (see Pl. 5, fig. 4, *S. Ao.*). The transverse part of the bulbus cordis forms a distinct characteristic prominence on the ventral surface of the heart; the proximal part has a well-developed circular musculature, while the muscular coat of the transverse and distal parts is poorly developed.

In the proximal portion of the bulbus there is, attached to the ventral wall, a solid ridge which extends to the transverse part (Pl. 5, figs. 1 and 3, *Sp. V. p.*) ; this ridge or valve is inserted along the middle line of the ventral bulbus wall, commencing at its posterior end a little anterior to, but immediately in line with, the interventricular septum (Pl. 5, figs. 1 and 2, *V. S.*, and *Sp. V. p.*) ; proximally it tapers off rapidly into the bulbus wall, but distally it broadens considerably, while its somewhat flattened end projects forwards into the lumen of the transverse part of the bulbus (Pl. 5, figs. 3 and 4, *Sp. V. p.*). On this valve near its origin there is always one distinct transverse ridge, in front of which again one or two more or less faint transverse furrows are usually to be distinguished (Pl. 5, figs. 1 and 3, *t. f.*) ; these recall the superimposed valves from which the spiral ridge is believed to have been evolved in phylogeny. At the same level, traces of vestigial pocket valves (17) are present on the lateral and dorsal walls of the bulbus cordis ; these are represented usually by three rows of tiny ridges arranged three in each row with still tinier irregular vestiges between (Pl. 5, figs. 1 and 3, *a, b, c*). In one case, out of eight hearts examined, only two vestigial valves could be distinguished in each row. The proximal ridges, those nearest the ventricle, are always most prominent.

As the transverse part of the bulbus is reached, the valvular ridge on the ventral wall of the first part is continuous with the ledge projecting from the dorsal wall of the transverse part (Pl. 5, figs. 1 and 4, *Sp. V. t.*). This vertical ridge in the transverse part is usually distinctly concave on its posterior surface, but in one instance it was characterised by the dorso-ventral flattening of its free ventral margin so as to give it in consequence a somewhat L-shape. In the distal part of the bulbus the valve becomes more flattened, has a free left border, and is attached along the right wall (Pl. 5, figs. 2 and 4, *Sp. V. d.*) ; these continuous valve-like structures curving along the length of the bulbus cordis constitute the spiral valve. In the distal part of the bulbus there is also a second longitudinal valve-like projection

attached along the left wall somewhat dorsally (Pl. 5, figs. 2 and 4, *B. R. 3.*) ; this unites for a short distance at its distal end with the spiral valve, dividing the cavity of the ventral aorta into a dorsal and ventral passage ; this short partition wall fuses at its distal extremity with the dorsal wall of the ventral aorta in front of the region of the fifth and sixth aortic arches, terminating in a little cushion-like projection (Pl. 5, figs. 2 and 4, *S. Ao.*). The result is the formation of a ventral passage communicating with the two anterior, and a dorsal passage communicating with the two posterior, pairs of aortic arches.

Coronary Arteries.—Two little arteries are present one on each side of the bulbus cordis. The right vessel is the larger ; it passes along the right wall of the distal part of the bulbus, dorsal to the transverse part, and then along the left wall of the proximal part, to the ventricle, where it is distributed. The smaller left artery supplies the left dorsal wall of the distal part of the bulbus. The course of these little vessels anterior to their appearance on the sides of the bulbus has not been traced, owing to the difficulty of dissecting the fibrous tissue in the region of the ventral aorta.

Summary.—The main features of importance in the anatomy of the heart of *Lepidosiren* may now be summarised, and some suggestions put forward as to their probable physiological significance.

In *Lepidosiren*, as we have seen, auricle, ventricle and bulbus cordis are each more or less incompletely divided into two right and left chambers, and as the septa of all these compartments (the proximal part only of the bulbus being considered for the moment) are approximately in the same plane, it follows, therefore, that the three chambers on the right and the three on the left are in sequence respectively. The sinus venosus opens into the right auricle, and its aperture is protected on the right side by a more or less efficient valve (Pl. 5, fig. 1, *r. S. A.*). The pulmonary vein opens directly into the left auricle and is also protected by a

valve-like fold (Pl. 5, fig. 2, *P. f.*). The auricles open into the ventricles round the margins of the auriculo-ventricular plug and there are no auriculo-ventricular valves apart from this (Pl. 5, figs. 1 and 2, *A. V. pl.*); the ventricular opening is guarded and closed from the side of the ventricle by the auriculo-ventricular plug; the bulbus cordis opens directly from the ventricle, and its aperture is undefended by any but the vestigial valves previously described (Pl. 5, figs. 1 and 3, *a, b, c*).

In the absence of direct physiological observations we may assume that the heart functions are as follows: venous blood from the sinus venosus and arterial blood from the pulmonary vein enters the right and left auricles respectively; when the auricles contract the sinu-auricular opening will be closed, partly by the action of the valve guarding its right side and partly by the bulging of the slack right wall of the pulmonary vein into it (Pl. 5, fig. 1, *P. f.*), while regurgitation along the pulmonary vein will be prevented partly by the action of the margins of the pulmonary aperture itself and partly by the marked obliquity of the pulmonary vein immediately before entering the auricular cavity (Pl. 5, fig. 2, *P. V.*); the contents of the auricles will then be discharged into the ventricles on either side of the auriculo-ventricular plug. With the contraction of the ventricles and of the interventricular septum the auriculo-ventricular plug is drawn in a ventral direction, and this, with the contraction of the muscles encircling it, closes the auriculo-ventricular aperture; simultaneously the proximal end of the bulbus is approximated to the interventricular septum, and the contents of either ventricle are discharged along the corresponding side of the spiral valve of the bulbus. On the contraction of the proximal muscular part of the bulbus cordis the two blood-streams are guided on either side of the septum of the first part to the transverse portion; in the transverse part of the bulbus the blood from the right side of the heart passes along the posterior channel behind the vertical septum, while the blood from the left side of the heart passes along the anterior

channel; this relationship is maintained in the third part of the bulbus where the venous stream passes dorsal to the two septa and so enters the posterior pair of aortic arches, while the arterial stream passes ventral to the septa and enters the anterior aortic arches (Text-fig. 1 and Pl. 5, fig. 4).

TEXT-FIG 1.

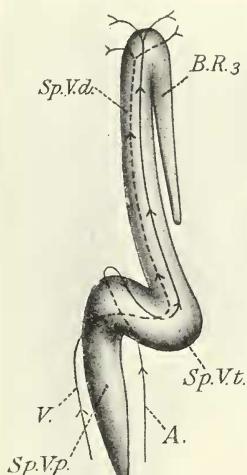


Diagram of valves in the bulbus cordis as seen from the ventral side. The line A indicates the course of the arterial blood, the line V that of the venous blood. *Sp. V.p.* Spiral valve on the ventral wall of the proximal part of the bulbus. *Sp. V.t.* Spiral valve on the dorsal wall of the transverse part of the bulbus. *Sp. V.d.* Spiral valve on the right wall of the distal part of the bulbus. *B. R. 3.* Longitudinal valve on the left wall of the distal part of the bulbus.

Owing to the very small amount of musculature in the walls of the middle and distal segments of the bulbus, the propulsive movement in those parts must be more an elastic recoil than an active contraction.

Regurgitation from bulbus to ventricle will be prevented partly by the plugging effect that the distal end of the prominent valve in the proximal part must have on a back-

wardly directed current (Pl. 5, figs. 1, 3 and 4, *Sp. V. t.*). Again at the distal end of the bulbus the anterior termination of the aortic septum does not taper off imperceptibly into the dorsal wall, but presents a solid vertical surface that would offer some resistance to regurgitation from the two anterior pairs of aortic arches (Pl. 5, figs. 2 and 4, *S. Ao.*).

It is of interest to note that the grooves formed between parts (1) and (2) and parts (2) and (3) of the bulbus are respectively homologous with the proximal and distal "Knickungsfurche" described by Greil in the developing bulbus cordis of *Lacerta* (9).

B. Arteries.

In the adult four afferent vessels arise in two sets of two in close proximity on either side, from the very short ventral aorta at the anterior end of the bulbus cordis (Pl. 5, fig. 1, *A. A.*).

Dorsally four efferent vessels join on either side to form the dorsal aortic roots, and these again, by their junction in the middle line, form the dorsal aorta (Text-fig. 2 *Ao.*); the two posterior pairs of afferent vessels arise somewhat from the dorsal surface of the ventral aorta, while the two anterior pairs are placed more ventrally. The proximal part of the anterior vessel on either side is really the paired ventral aorta, which, after passing a short distance outwards and forwards in the floor of the mouth, is prolonged into the lingual artery (Text-fig. 2, *L. A.*) anteriorly, immediately posterior and external to which it gives off the third aortic arch (the most anterior of the persisting aortic arches). In the adult this aortic arch (Text-fig. 2, *A. A. 3*) curves outwards dorsally and backwards and then inwards to the outer margin of the roof of the mouth, where it joins the dorsal aortic root at the point of origin of the dorsal carotid artery (Text-fig. 2, *Car.*). The dorsal root then passes inwards and slightly backwards, and is joined in rapid succession, a short distance from the middle line, first by the fourth, and then by the short

TEXT-FIG. 2.

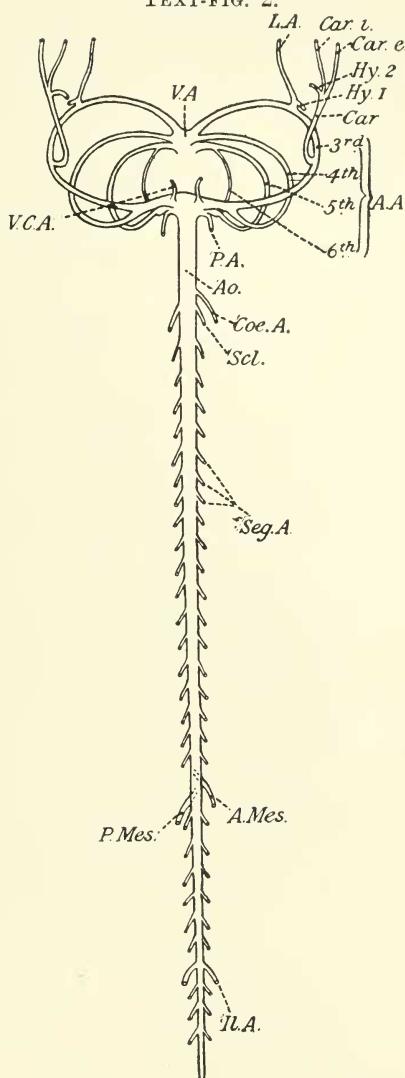


Diagram of arterial system, dorsal view. *AA.* 3, 4, 5, 6. The four aortic arches. *A. mes.* Anterior mesenteric artery. *Ao.* Aorta. *Car.* Dorsal carotid. *Car. e.* External branch of carotid. *Car. i.* Internal branch of carotid. *Coe. a.* Cœeliac artery. *Hy. 1.* Branch to hyoidean hemibranch. *Hy. 2.* Hyoidean efferent artery. *Il. A.* Iliac artery. *L. A.* Lingual artery. *P. A.* Pulmonary artery. *V. C. A.* Vertebral-cerebral artery. *P. mes.* Posterior mesenteric artery. *Scl.* Subclavian artery. *Seg. A.* Segmental arteries. *V. A.* Ventral aorta.

common stem of the fifth and sixth aortic arches. In the middle line the dorsal aortic roots meet and form the dorsal aorta (Text-fig. 2, *Ao.*). The fourth pair of aortic arches takes origin from the proximal part of the lateral ventral aorta on either side and curves outwards, upwards and inwards to its junction with the dorsal aortic root. The fifth and sixth pairs arise by short common stems from the proximal part of the ventral aorta. From these common stems the sixth aortic arches, which are short and of extremely small calibre, are given off almost immediately. The fifth and sixth aortic arches on either side curve round the postero-lateral regions of the mouth-cavity, and rejoin one another dorsally, entering the dorsal aortic roots near the middle line by a short common stem. The small size of the vessels of the sixth aortic arches is correlated with the fact that in the adult *Lepidosiren* the pulmonary arteries no longer arise directly from them as they did in the larva, but from the common stems of the fifth and sixth arches on either side, and apparently the fifth arch has taken on the larger share of the blood supply, while the sixth arch has dwindled to a very insignificant vessel. The channel by which arches 5 and 6 communicate with the dorsal aorta is relatively small compared with the lumen of the pulmonary artery, the main blood-stream passing into the latter vessel. In *Lepidosiren* all the aortic arches can be traced throughout as definite uninterrupted vessels.

Vertebro-cerebral Arteries.—Immediately before the dorsal aortic roots join to form the dorsal aorta, two little vessels, the vertebro-cerebral arteries, pass from them one on either side to the base of the skull (Text-fig. 2, *V.C.A.*).

Dorsal Aorta.—The dorsal aorta (Text-fig. 2, *Ao.*) is formed by the junction of the dorsal aortic roots far forwards about the level of the junction of the distal and transverse portions of the bulbus cordis. It extends throughout the length of the spinal column immediately ventral to it, and in the caudal region lies in the haemal canal, dorsal to the caudal vein. The main vessels arising from the dorsal aorta are the coeliac, subclavian, anterior and posterior

mesenteric and the iliac arteries (Text-fig. 2, *Cœ. A.*, *Scl.*, *A. mes.*, *P. mes.*, and *Il. A.*). Of these the limb vessels are paired, the others unpaired. Posterior to the subclavian arteries the aorta gives off segmentally arranged vessels (Text-fig. 2, *Seg. A.*), which in turn give branches to the spinal column, body-walls, and to the kidney and gonad.

Lingual Arteries.—On either side the paired ventral aorta is prolonged forwards as the lingual artery (Text-fig. 2, *L. A.*); this vessel passes outwards and forwards along the floor of the mouth between the ramus of the jaw, to which it gives a branch, and the tongue.

Carotid Arteries.—The dorsal aortic root on either side is prolonged forwards as the dorsal carotid artery (Text-fig. 2, *Car.*); this vessel passes forwards a short distance in the roof of the mouth, as far as the anterior part of the auditory capsule; here it divides into an internal and an external branch (Text-fig. 2, *Car. i.*, *Car. e.*). The external branch passes forwards slightly dorsally and outwards, accompanying the trigeminal nerve, with which it is distributed to the surface of the head. The internal branch passes dorsally a little, to the base of the brain itself.

Pulmonary Arteries.—Two pulmonary arteries (Text-fig. 2, *P. A.*) arise one on either side from the short common dorsal stem of the fifth and sixth aortic arches; both vessels extend for some distance dorsal to the oesophagus on either side of the aorta, but as they reach the lungs their positions relative to one another alter. Of the two vessels the left artery is the larger; it passes backwards and inwards and curves from the left side round the ventral surface of the oesophagus to reach the ventral surface of the lungs, and then, after crossing ventrally to the left pulmonary vein, bifurcates, giving a branch to each lung. The right pulmonary artery is the smaller: on reaching the lungs it passes backwards and inwards, to the left of and ventrally to the cœliac artery, and divides into two branches, one to the dorsal surface of each lung.

Cœliac Artery.—The cœliac artery (Text-fig. 2, *Cœ. A.*)

arises from the dorsal aorta on the right side a short distance behind the point of junction of the two aortic roots. It passes first ventrally, then posteriorly, along the right outer angle of the liver, and crosses the ventral surface of that organ to reach the tip of the gall-bladder, dorsal to which it finally reaches the intestine, in the wall of which it is distributed.

Subclavian Arteries.—Two small vessels, the subclavian arteries (Text-fig. 2, *Scl.*), arise one on either side of the aorta immediately posterior to the cœliac artery and pass outwards to supply the pectoral limbs.

Anterior Mesenteric Artery.—This vessel (Text-fig. 2, *A. mes.*) arises from the mesial ventral surface of the dorsal aorta far back, a short distance in front of the iliac arteries, and passes in the mesentery to reach the walls of the intestine, to which it is distributed.

Posterior Mesenteric Artery.—Immediately posterior to the anterior mesenteric artery a second vessel, the posterior mesenteric (Text-fig. 2, *P. mes.*), arises also from the mesial ventral surface of the dorsal aorta and passes through the mesentery to the intestine, to which it also is distributed.

Iliac Arteries.—Posteriorly two small vessels (Text-fig. 2, *Il. A.*) arise from the dorsal aorta near its caudal extremity and are distributed, one on either side to the pelvic limbs.

c. Veins.

Ductus Cuvieri.—A short transverse ductus Cuvieri opens into the anterior part of the sinus venosus (Text-fig. 3, *S. V.*) on either side ; these vessels are formed by the junction of the anterior and posterior cardinal veins (Text-fig. 3, *r. D. C.* and *l. D. C.*).

Anterior Cardinal Veins.—On each side an anterior cardinal vein (Text-fig. 3, *A. Car.*) passes back superficially from the front of the upper jaw, receiving an anterior cerebral vein in front of, and an orbital vein immediately behind, the eye, beneath which organ it passes : it also receives a vessel from the surface of the lower jaw at the angle of the mouth. Posteriorly a venous trunk, the posterior cerebral vein (Text-

TEXT-FIG. 3.

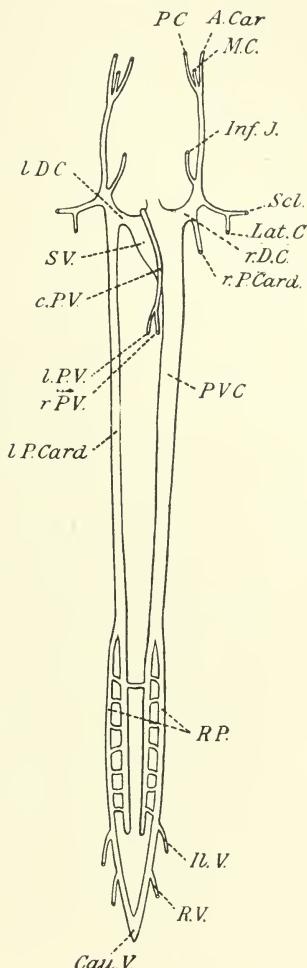


Diagram of venous system, dorsal view. *A. Car.* Anterior cardinal. *Cau. v.* Caudal vein. *c. P. V.* Common pulmonary vein. *Il. V.* Iliac vein. *Inf. J.* Inferior jugular. *Lat. C.* Lateral cutaneous. *l. D.C.* Left duct of Cuvier. *l. P.V.* Left pulmonary vein. *l. P. Card.* Left posterior cardinal. *M.C.* Vestige of median cephalic vein. *P.C.* Posterior cerebral vein. *P. V. C.* Posterior vena cava. *r. D. C.* Right duct of Cuvier. *R. P.* Renal portal vein. *r. P. Card.* Right posterior cardinal. *r. P. V.* Right pulmonary vein. *R. V.* Rectal vein. *Sel.* Subclavian. *S. V.* Sinus venosus.

fig. 3, *P. C.*), passes backwards and outwards from the inside of the skull, and then turns sharply in a ventral direction to join the anterior cardinal at the lower part of, and posterior to, the auditory capsules. At the junction of the cerebral vein with the anterior cardinal they are joined by a third very wide short vessel (Text-fig. 3, *M. C.*), passing between the skull and the surrounding musculature, which is apparently a vestige of the median cephalic vein present in the embryo. From this point the cardinal vein passes ventrally and a little inwards, curving backwards, dorsal to the aortic arches, to be joined on the dorsal surface of the pericardium by the subclavian and inferior jugular veins (Text-fig. 3, *Inf. J.* and *Scl.*) before joining the posterior cardinal vein (Text-fig. 3, *l. and r. P. Card.*) to form the duct of Cuvier (Text-fig. 3, *r. D. C.* and *l. D. C.*).

Inferior Jugular Veins.—On either side of the floor of the mouth an inferior jugular vein (Text-fig. 3, *Inf. J.*) passes backwards below the afferent branchial vessels along the roof of the pericardium, and joins the respective anterior cardinal on its inner ventral surface near the anterior end of the ductus Cuvieri.

Subclavian Veins.—From each pectoral limb a vein passes inwards and forwards to join the anterior cardinal vein near the junction of that vessel with the inferior jugular vein (Text-fig. 3, *Scl.* and *Inf. J.*).

Caudal and Renal Portal Veins.—A caudal vein (Text-fig. 3, *Cau. V.*) runs beneath the caudal aorta enclosed in the hæmal canal. On emerging from this it divides to form the paired renal portal veins (Text-fig. 3, *R. P.*), which pass along the outer ventral margins of the kidneys to terminate at their anterior ends and anastomose through the substance of the kidney with the left posterior cardinal and the posterior vena cava (right posterior cardinal) respectively (Text-fig. 3, *l. P. Card.* and *P. V. C.*).

Iliac Veins.—Two iliac veins from the pelvic limbs enter the renal portal veins, one on either side, shortly after these enter their respective kidneys (Text-fig. 3, *Il. V.*).

Left Posterior Cardinal Vein and Posterior Vena Cava.—The left posterior cardinal vein and the posterior vena cava (right posterior cardinal) appear on the dorso-mesial surfaces of the posterior part of the left and right kidneys respectively; they communicate through these organs by an intricate meshwork of venous capillaries with the left and right renal portal veins (Text-fig. 3, *l. P. Card.* and *P. V. C.*).

The left posterior cardinal vein, on leaving the kidney, passes forwards between the intestine and the body-wall ventrally to the left lung, and passing along the left of the roof of the sinus venosus, joins the posterior termination of the left anterior cardinal vein to form the left duct of Cuvier (Text-fig. 3, *l. D. C.*).

The posterior vena cava (right posterior cardinal vein) passes forwards from the right kidney, and inclining somewhat to the middle line, is embedded in the dorsal surface of the liver; here it receives a number of venous radicles from the liver substance. Immediately on emerging from the anterior end of the liver it enters the sinus venosus (Text-fig. 3, *P. V. C.*). In the one adult injected Lepidosiren in which this part was dissected, there was only one large transverse anastomosis towards the posterior part of the liver, between the left posterior cardinal vein and that part of its fellow on the right side that forms the hind part of the posterior vena cava (13). Hyrtl mentions four such anastomoses in an adult specimen.

The renal portal veins posteriorly and the left posterior cardinal and posterior vena cava anteriorly receive veins from the body-walls and also vertebral veins. These are segmentally arranged.

Right Posterior Cardinal Vein.—The anterior portion of the right posterior cardinal vein (Text-fig. 3, *r. P. Card.*) is present as a short vessel near the posterior end of the heart; it receives a vein from the region of the vertebral column and one from the body-wall, and the trunk so formed joins the posterior part of the right anterior cardinal vein to form the right duct of Cuvier. A small vertebral vessel joins the left posterior cardinal vein also in this region.

Pulmonary Veins.—Posteriorly the pulmonary veins lie along the outer borders of the lungs, but turn inwards at about the anterior third of those organs across their ventral surfaces, and join to form the common pulmonary vein (Text-fig. 3, *c. P. V.*) somewhat to the right of the middle line. The common pulmonary vein passes forwards and to the left on the dorsal wall of the anterior portion of the posterior vena cava, and entering the pericardium reaches the roof of the sinus venosus. It then runs obliquely to the left in the roof of the sinus venosus and curves ventrally across the anterior end of the sinus, to open into the left auricle on the left side of a fold that projects into the auricles, across the middle of the dorsal surface of the auriculo-ventricular plug (Pl. 5, fig. 1, *P. f.*). This pulmonary fold is continuous dorsally with the auricular roof, anteriorly with the muscular part of the auricular septum, and ventrally with the auriculo-ventricular plug. The pulmonary aperture is a rounded opening in the left wall of this pulmonary fold, and is guarded by a hood-like flap that serves to guide the blood directly to the left on entering the auricle (Pl. 5, fig. 2, *P. V.* and *P. f.*).

Coronary Vein.—A small coronary vein passes from about the middle of the dorsal surface of the right ventricle to reach the floor of the sinus venosus a short distance from the sinu-auricular aperture; its opening is guarded by a valvular flap whose free border is directed posteriorly. The exact point at which this little vessel passes from the ventricle to the sinus varies considerably in different specimens (Plate 5, fig. 1, *C. V.*).

III. DEVELOPMENT OF THE HEART.

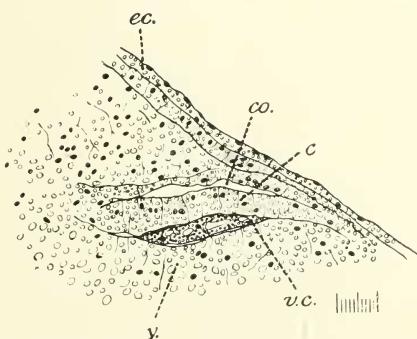
Pericardiac Space.—At Stage 23, in the development of *Lepidosiren*, when there are twenty-four segments present, the lateral mesoderm is extending ventrally and inwards over the surface of the yolk on either side of the endodermic pharyngeal rudiment, and already two chink-like cœlomic

splits are present, one on either side, between its layers (Text-fig. 4, *co.*).

These two folds of mesoderm, with their contained chinks, soon extend across the surface of the yolk, and meeting in the middle line, ventral to the pharyngeal rudiment, fuse to form the pericardiac portion of the cœlom (Stage 24, Text-fig. 5 *a*, *b* and *c*, *spl. m.* and *som. m.*).

Owing to the spherical shape of the yolk and to the close

TEXT-FIG. 4.¹



Transverse section, Stage 23. Cœlom just appearing, columnar splanchnic mesoderm defined, vessel cells present. *c.* Columnar layer of mesoderm. *co.* Cœlom. *ec.* Ectoderm. *v. c.* Vessel cells. *y.* Yolk.

approximation of the embryo round it, the pericardiac cœlom is, from the first, flattened, while it is curved transversely round the anterior surface of the yolk, and also dorsally a little on either side of the pharyngeal rudiment. Thus this part of the cœlom is somewhat crescent-shaped, with the pharyngeal endoderm resting between its horns, and also a little concave posteriorly owing to the curvature of the yolk. The walls of the pericardiac cavity consist of a single layer of cells, of which those of the splanchnic wall are distinctly columnar in shape, giving rise later to the myocardium, while those of the somatic wall are comparatively flattened cells from which the parietal pericardium is derived.

¹ Each division of the scale in this and succeeding figures represents .01 mm.

Rudiments of the Vitelline Veins, Heart and Aorta.—Simultaneously, with the progressive delamination of the anterior margins of the lateral mesoderm from the surface of the yolk, two slender irregular strands of cells (Text-fig. 4, *v. c.*) appear, one on either side, between the yolk and the splanchnic layer of mesoderm. These are em-

TEXT-FIG. 5.

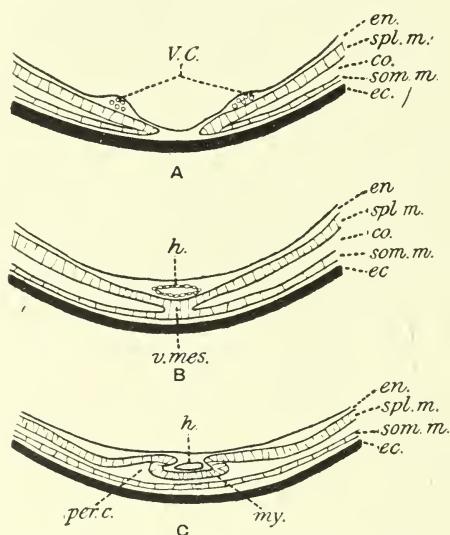
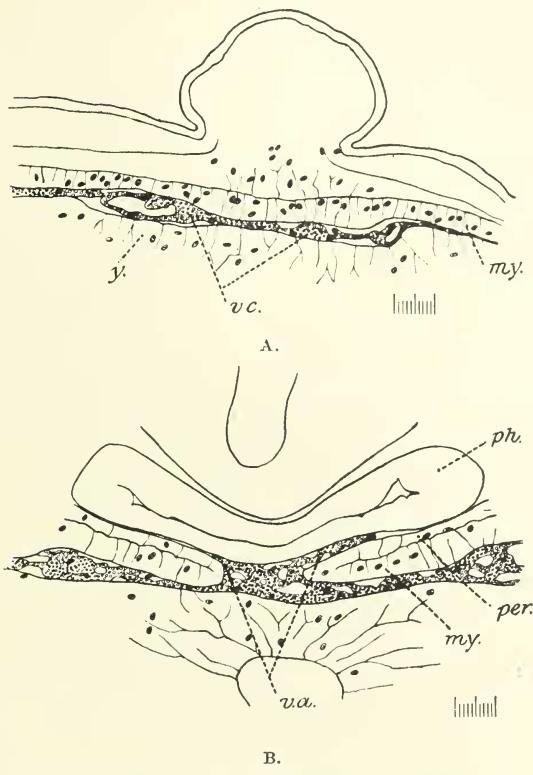


Diagram illustrating the relations of the heart-rudiment to the mesoderm layers and coelom. *co.* Coelom. *ec.* Ectoderm. *en.* Endoderm yolk. *h.* Heart. *my.* Myocardium. *per. c.* Pericardial coelom. *som.m.* Somatic mesoderm. *spl.m.* Splanchnic mesoderm. *V. C.* Vessel cells. *v.mes.* Ventral mesocardium.

bryonic endothelial cells, and they extend inwards across the anterior surface of the yolk simultaneously with the development of the mesoderm and coelom. These cells are comparatively large and heavily yolked, and except peripherally, where they are continuous with the inner mesoderm layers over the lateral surfaces of the yolk, they are quite distinct from the endoderm and mesoderm, between which they lie.

With the fusion of the mesoderm below the ventral surface of the pharynx and the formation of the bilateral

TEXT-FIG. 6.



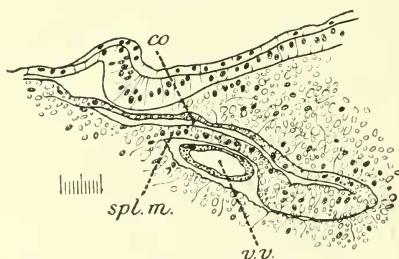
A. Section transverse to the heart-rudiment at Stage 24. B. Section transverse to the heart, showing endothelial rudiments of the paired ventral aortæ. *my.* Myocardium. *per.* Outer wall of pericardiac cavity. *ph.* Pharyngeal rudiment. *v.a.* Rudiment of the paired ventral aortæ. *v.c.* Vessel-cells with unexpanded cardiac cells between them. *y.* Yolk.

pericardiac cœlom, the two endothelial strands meet on the anterior surface of the yolk, and form a little single-layered sheet of endothelial cells forming the rudiment of the heart (Stage 24, Text-fig. 6 A, *v.c.*).

This fusion of the mesoderm below the pharynx occurs

over a very short space, and the heart-rudiment is correspondingly short also. A trifle later (Stage 24 +), a strand of embryonic endothelial cells is found, continuous with and anterior to the heart-rudiment immediately ventral to the pharyngeal rudiment, and from it again two similar strands pass, one on either side, sharply outwards and a little backwards and dorsally to the sides of the head between the parietal pericardium and the lateral expansions of the pharyngeal rudiment: these prolongations are the rudiments of the lateral ventral aortæ (Text-fig. 6B, *v. a.*). Intra-cellular

TEXT-FIG. 7.



Expanding vitelline vessel and splanchnic layer of mesoderm bulging forwards into the coelom. *co.* Cœlome. *spl.m.* Splanchnic mesoderm. *v.v.* Vitelline vessel.

spaces, due to metabolic processes accompanied by the secretion of fluid, soon form in these various embryonic cells in the order of their appearance, that is to say, first in the vitelline veins, then in the heart, and finally in the rudiments of the ventral aortæ (Text-figs. 4, 6A and B, *v. c.* and *v. a.*). These spaces increase in size, adjacent cells coalesce, and finally definite endothelial vessel-tubes result (Text-fig. 7, *v. v.*).

Simultaneously with the expansion of the endothelial tubes the splanchnic mesoderm bulges before them into the coelomic cavities and affords a covering to the developing vessels (Text-fig. 7, *spl.m.*). As the middle cells of the heart-rudiment vacuolate and expand a trifle later than those at its lateral margins (Text-fig. 6A, *v.c.*), it has for a while a somewhat dumb-bell-like appearance on horizontal section,

but this condition is transitory, though the flattened oval shape of the lumen of the heart-tube—attributable probably to the spherical surface of the yolk and the close approximation of the embryo against it—persists for a considerable time.

This characteristic arrangement of the rudiments of the vitelline veins, heart and ventral aorte is probably due to the presence of the yolk. Instead of being extended in the long axis of the embryo with the rudiments of the great vessels appearing far apart at either end of it, the heart-rudiment has suffered an approximation of its cranial and caudal extremities, while the intervening part has become folded on itself and projects ventrally over the yolk. This arrangement, therefore, is merely an expression of the relations of embryo and yolk peculiar to *Lepidosiren*.

Shape and Attachments of the Heart.—From the first the heart-rudiment is much flattened between the head of the embryo and the yolk, and the comparative approximation of its two ends is maintained throughout development. This, as already suggested, is determined by the presence of the yolk and by the flattened, laterally expanded shape of the pericardiac space, both of which conditions, of course, are interdependent and persist for a comparatively long time. These factors also account for the vertical position of the heart, relative to the long axis of the embryo, during its earlier stages of development.

When the mesoderm plates meet ventrally in the cardiac region they fuse rapidly, and the extremely short ventral mesocardium disappears almost as soon as formed (Stage 24 +, Text-fig. 5b, *v. mes.*). The heart now grows rapidly in length, and as its anterior and posterior ends remain relatively fixed it projects ventrally more and more into the narrow pericardiac space and forms a loop, flattened antero-posteriorly (Text-fig. 8). This rapid growth of the heart-tube, combined with the peculiar shape of the cavity in which it is placed, causes a degree of twisting, the immediate effect of which is to free the loop from the dorsal mesocardium, so that now the heart has a complete myocardiac covering, only the dorsal

wall of the developing sinus venosus being still in close relationship with the pharyngeal rudiment above. In this adjustment of the heart-tube to the pericardiac space, the descending and ascending limbs of the loop, from being posterior and anterior respectively, come to lie side by side, the former on the left and the latter on the right (Text-fig. 8). That is to say, the anterior and posterior ends of the heart are fixed, but the loop as a whole rotates approximately through a right angle in a clockwise direction as seen in a dorsal view of the heart, thus twisting the long axis of that organ into a position approximately transverse to, instead of parallel with, the axis of the embryo. This position is maintained

TEXT-FIG. 8.

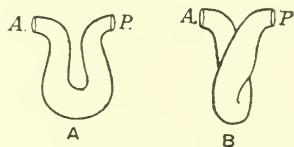


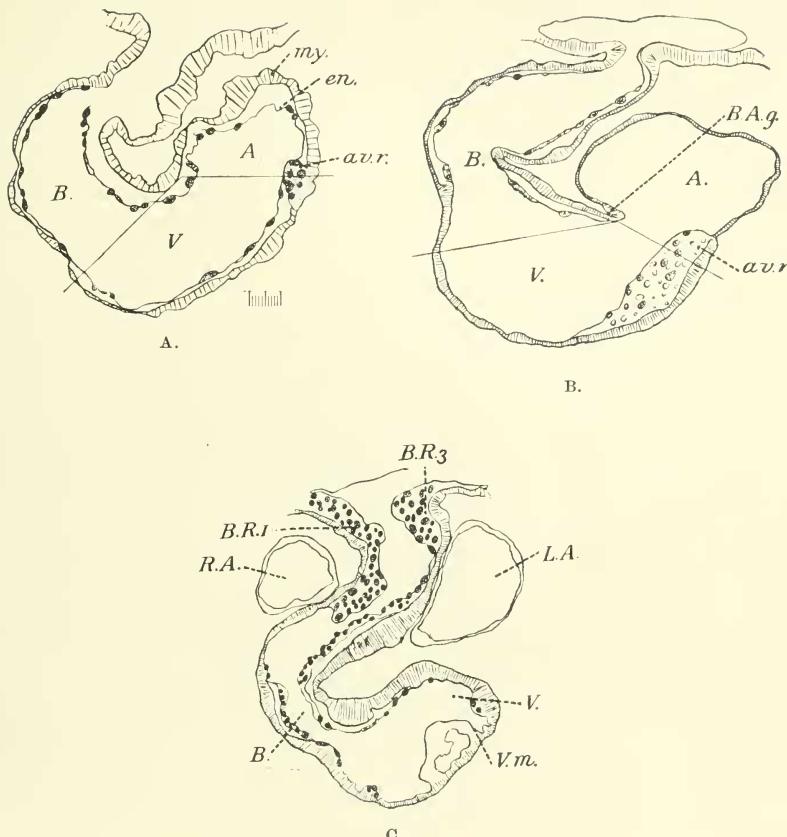
Diagram to illustrate the looping of the heart on itself; (A) represents the primitive and (B) the secondary position of the heart.
A. Anterior. *P.* Posterior.

till the maximum vertical development of the heart has been attained, when a degree of untwisting occurs as the pericardiac space begins to increase rapidly in antero-posterior depth, and the adult form and position of the heart are reached.

From Stage 25 the heart consists for a time of a double-walled tube, the inner wall being endothelial and the outer myocardial (Text-fig. 9).

The tube is bent in a narrow **U**-shape, its anterior and posterior ends being in close proximity to one another, and both approximately in the middle line, the former terminating on either side in the lateral ventral aorta, the latter forming the sinus venosus, somewhat to the right. This double **U**-tube may be divided into four parts: (1) A posterior descending auricular part (Text-fig. 9 *A*, *A.*), the axis of which forms

TEXT-FIG. 9.

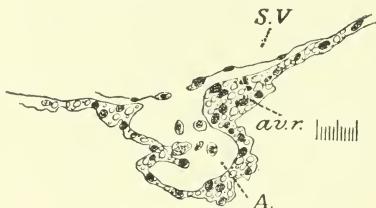


Sections transverse to the body of the embryo, illustrating the development of the heart. A. Stage 28. Heart markedly U-shaped, endothelium and myocardium still separate. The straight lines demarcate approximately the different divisions of the heart. B. Stage 30. C. Stage 31. A. Auricle. a.v.r. Auriculo-ventricular ridge, which in fig. B extends to the ventral curvature of the ventricular part of the heart. B. Bulbus. B.A.g. Bulbo-auricular groove. B.R.1. Right bulbus ridge. B.R.3. Left bulbus ridge. en. Endothelium. L.A. Left auricle. my. Myocardium. R.A. Right auricle. V. Ventricle. V.M. Ventricular musculature continuous posteriorly with the auriculo-ventricular ridge.

almost a right angle with the sinus venosus and projects to the left into the pericardiac cavity; (2) a short auricular canal intervening between (1) and (3); (3) a ventral, transverse, ventricular part (Text-fig. 9 *a*, *V.*) directed from left to right, and (4) an anterior, ascending part, curving from right to left towards the middle line again—the forerunner of the bulbus cordis (Text-fig. 9 *b*, *B*). The long ventral and short dorsal walls of the transverse part of the tube may now, for brevity, be called the ventral and dorsal curvatures of the heart respectively.

Auriculo-ventricular Plug.—At Stage 27, before there is any definite division of the heart into separate

TEXT-FIG. 10.



Section through the sinu-auricular junction at Stage 28. *A.* Auricle. *av. r.* Auriculo-ventricular ridge. *S. V.* Sinus venosus.

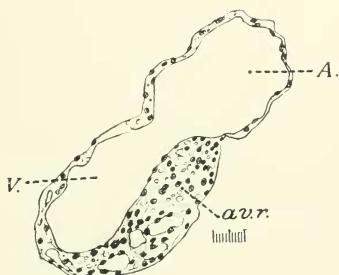
chambers, a little knot of cells appears between the two layers of the heart-wall, at the left ventral margin of the opening of the sinus venosus into the auricle (Text-fig. 10, *av. r.*).

This knot of cells forms a ridge extending in a ventral direction along the left posterior wall of the heart through the auricular canal, and reaching as far as the commencement of the ventral curvature (Text-figs. 9 *a* and *b*, *av. r.*) On the ventral curvature the tip of the ridge comes in contact and becomes continuous with the muscle-fibres appearing in the ventricle (Text-fig. 11, *av. r.*). This ridge inclines from left to right (compare fig. 15*a*, *b*, and *c*, *av. r.*) and divides the auricle into a larger right and a smaller left compartment, the former being situated at first somewhat posterior to the

latter. The sinu-auricular aperture opens on the right of the ridge and is therefore confined to the right auricle. Throughout, the right auricle remains the larger, though the left expands rapidly—as does also the left ventricle—after the development of the pulmonary vein.

Division of the Heart into Chambers.—As development proceeds the various chambers of the heart come to be demarcated from one another; this is largely brought about by a marked disproportion in the rates of growth at different parts. For a time growth occurs chiefly in

TEXT-FIG. 11.



Sagittal section through the heart at Stage 30. *A.* Auricle. *av. r.* Auriculo-ventricular ridge becoming continuous with muscular tissue in the ventricle. *V.* Ventricle.

length and width; a little later, however, the pericardiac cavity increases in anteroposterior depth, more especially in its ventral part, and this allows the heart, as already mentioned, to regain a position approximately parallel with, instead of transverse to, the long axis of the embryo. In fact from this stage till the permanent condition is attained—as the liver develops and retreats somewhat towards the tail, as the left auricle and ventricle expand with the appearance of the pulmonary vein, as the yolk is absorbed and the adult shape of the anterior part of the body is reached—a certain rotation of the loop takes place. The heart loop gradually swings back again in a counter-clockwise direction, as seen in a dorsal view, about an axis perpendicular to the long

axis of the embryo, till, from being practically at right angles to, the heart loop is once more parallel with, the length of the embryo (Pl. 5, figs. 5, 6 and 7). Throughout it must be remembered that the anterior and posterior ends of the heart, are fixed, and therefore whatever rotation occurs affects only the loop of the tube, and further, that the second rotation is merely a recovering of the original position of the primitive endothelial rudiment before its peculiar environmental relations compelled it to adopt a transverse position. Ultimately, therefore, the amount of twisting displayed by the heart as a whole is negligible. Also as the yolk disappears, the heart, from being vertical (Text-figs. 9 and 12), becomes more and more horizontal in position, the ventricular axis coming to form a comparatively acute angle with the common axis of sinus and auricle (Pl. 5, fig. 1). Thus in *Lepidosiren*, owing to the exigencies of the yolk, the definitive position of the heart is not finally assumed till a fairly late stage in development is reached, which renders a description of its changing anatomical relations peculiarly difficult. In the meantime, however, for the sake of simplicity, the heart will be considered as vertical to the long axis of the embryo, the position which is maintained more or less till development is practically complete, and with its loop rotated into the definitive antero-posterior position. The terms "anterior" and "posterior" thus express in the earlier stages relationships that in the adult are ventral and dorsal respectively.

The auricular part of the heart now expands dorsally and laterally but more especially laterally, and comes to bulge on either side round the conus (compare Text-fig. 9 A, B and C, A); it also gradually expands on either side of the sinus venosus ventral to the ducts of Cuvier, and overlaps the unexpanding auricular canal anteriorly and laterally.

The posterior auricular wall, however, on which the auriculo-ventricular ridge has appeared, takes little part in this general enlargement, with the result that it remains comparatively short, and the sinus-auricular and auriculo-ventricular openings, which are situated at either end of it, remain com-

paratively close to one another. In Lepidosiren the auricular canal is only a transitory division of the heart externally, and early merges its identity in the auriculo-ventricular aperture; in the adult its wall is represented by a little flattened muscular band, that passes round the rim of the auriculo-ventricular opening on to the dorsal auricular wall, on which is situated the auriculo-ventricular plug.

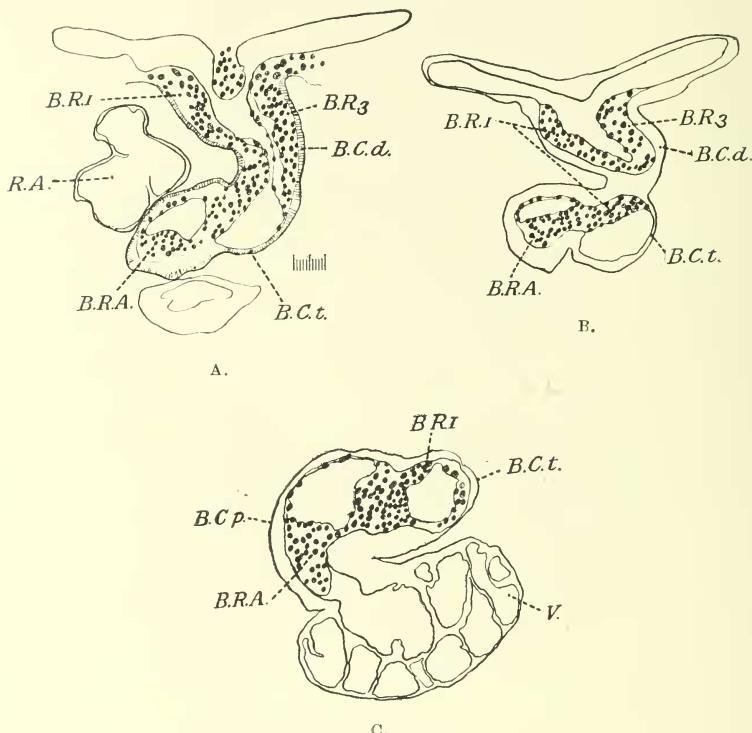
The ventral and lateral walls of the transverse part of the heart expand rapidly (Pl. 5, figs 5 and 6, *V.*) while the dorsal curvature and the distal part of the ventral curvature of the heart form the proximal part of the bulbus cordis (compare Text-fig 9, *a*, *b* and *c, B.*). The ventricle proper is formed by the expansion of the ventral and lateral walls of the transverse part of the heart between the auriculo-ventricular and ventriculo-bulbar apertures, causing it to bulge laterally and a little posteriorly round the auricular canal and laterally and anteriorly round the proximal part of the bulbus cordis. For a time the ventricular part of the heart is considerably tilted to the left, but with the swinging of the bulbus to the front and the development of the interauricular and interventricular septa, this gradually disappears, and in the adult the ventricle is approximately symmetrically placed about the middle line (Pl. 5, figs. 5, 6 and 7, *V.*).

A general increase occurs in the dimensions of the bulbus cordis also, but this expansion is most marked in its middle part (Text-fig. 9*A*, *B*, and *c, B.*), affecting particularly the anterior and left walls of this region (Pl. 5, figs. 5 and 6, *B.*). The distal segment, on whose right wall the right septum has appeared reaching along the middle part as far as the proximal part of the bulbus, and on whose left wall the shorter left septum is present (Text-fig. 9*c, B. R. 1* and *B. R. 3.*), undergoes a much lesser degree of expansion. The narrow tubular character of the proximal part of the bulbus formed by the dorsal curvature of the heart and the distal segment of the ventral curvature has already been referred to.

The bulbus as a whole, however, is now rapidly increasing

in length, and this, combined with the localised expansion of its middle part round the comparatively unyielding right

TEXT-FIG. 12.



A. Section through the bulbus cordis at Stage 32, showing continuity of bulbus ridges 1 and *A*. B. Section through the bulbus at Stage 32, showing continuity of bulbus ridges 1 and *A*, along the transverse part of the bulbus. C. Section through the ventricle and the proximal end of the bulbus at Stage 31, showing continuity of bulbus ridge 1 and *A*, along the posterior (dorsal) wall of the transverse part of the bulbus. *B. C. d.* Distal segment of bulbus. *B. C. p.* Proximal segment of the bulbus. *B. C. t.* Transverse segment of bulbus. *B. R. 1.* Right bulbus ridge. *B. R. 3.* Left bulbus ridge. *B. R. A.* Ridge on anterior (ventral) wall of proximal segment of the bulbus. *R. A.* Right auricle. *V.* Ventricle.

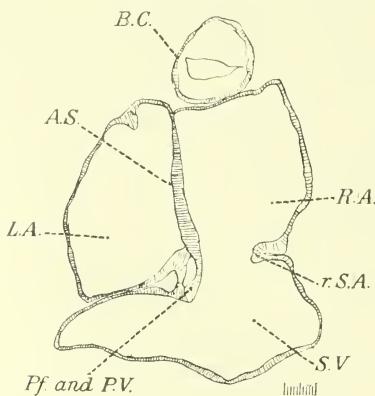
wall, causes it to kink abruptly on itself in this middle region, and gives the expanding part the appearance of being

frilled on across the long axis of the bulbus cordis (compare Pl. 5, figs. 5, 6 and 7, *B. C. t.*, also Text-fig. 12A, B and C, *B. C. t.*). Thus a distinct bulging towards the left—the side away from the septum on the right wall—occurs, causing a marked external constriction¹ on this side between the proximal and middle parts of the bulbus (Pl. 5, figs. 5, 6 and 7, *P.*). As the bulging tapers more gradually towards its distal end, the third part of the bulbus is demarcated externally from the middle part by a less abrupt constriction¹ on the right side (Pl. 5, figs. 5, 6 and 7, *D.*). This kinking and asymmetrical expansion of the middle part of the originally comparatively straight bulbus results in the formation of the transverse segment, and the original right wall of this part adopts a transverse posterior (dorsal in terms of the adult) position. Similarly, that part of the right septum situated on the right wall of this region of the bulbus becomes correspondingly displaced, and extends, transversely to the long axis of the bulbus, along what has become the posterior (dorsal) wall of the middle part (Text-fig. 12c, *B. R. 1.*). If the two ends of a straight perpendicular tube be approximated to one another so as to form a transverse kink about the middle of its length, it will be found that the right wall of the upper part is continuous with the upper wall of the transverse part, that is, with what was originally the right wall of the middle part. If now the transverse part expand forwards and upwards round its unextending upper wall, that wall—and any structure on its inner surface—will come to occupy a somewhat posterior position. This is apparently what happens in the development of the bulbus cordis of *Lepidosiren*. The gradual rotation of the definitive long axis of the heart into a position parallel with the long axis of the embryo must again be recalled, which, while the distal end remains fixed, swings

¹ Proximal and distal *Knickungsfurche* of the developing bulbus cordis of *Lacerta*.—Greil, A., “Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Herzens und des Truncus arteriosus der Wirbeltiere,” ‘Morph. Jahrb.,’ Bd. 31, 1903.

the proximal part of the bulbus round to the left (Pl. 5, figs. 5, 6 and 7). This, combined with the presence of the expanding auricles, probably assists in determining the bulging of the middle part mainly in an anterior direction and to the left. The bulbus has now attained its adult form, and lies cushioned against the auricles, appearing to indent them, with its posterior (dorsal) wall very intimately related to their anterior (ventral) surfaces (Pl. 5, fig. 7).

TEXT-FIG. 13.



Horizontal section through the heart at Stage 32. *S. V.* Sinus venosus. *r. S. A.* Right sinu-auricular fold. *R. A.* Right auricle. *B. C.* Bulbus cordis. *A. S.* Auricular septum. *L. A.* Left auricle. *Pf.* Incipient pulmonary fold. *P. V.* Pulmonary vein.

By Stage 32 the demarcation of the various chambers from one another is achieved, and their various orifices more or less clearly defined.

The sinu-auricular opening remains, as before, a circular aperture opening into the auricular chamber on the right and having the auriculo-ventricular ridge with the developing pulmonary fold (Text-fig. 13, *P. f.*) on the left. The bulging of the right auricle along the right side of the sinus venosus, as already mentioned, gives rise to a constriction externally between the two chambers, that is represented in the interior of the heart by a fold guarding the right side of

the sinu-auricular opening (Text-fig. 13, *r. S. A.*). Dorsally this fold is lost on the auricular roof, while ventrally it curves round on to the right side of the auriculo-ventricular ridge. The development of this right sinu-auricular fold is therefore identical with that of the similar right venous valve in Elasmobranchs (21).

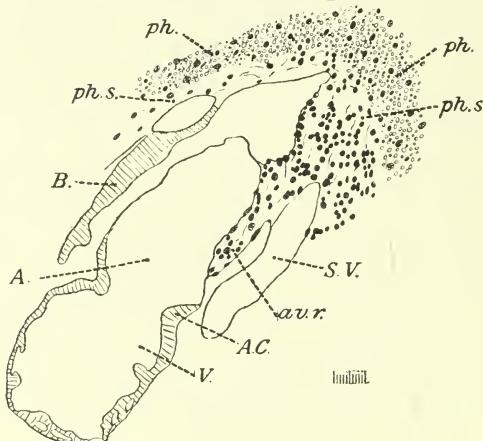
The auriculo-ventricular aperture is defined by the marked localised bulgings of the auricle and ventricle on either side of the extremely short auricular canal. The auricles expand markedly over the dorsal curvature of the heart, while the comparatively much slighter degree of ventricular expansion occurs wholly along the ventral curvature (Text-fig. 9 *B*). This disproportion of growth results in a marked constriction externally, that is manifested in the interior of the heart by the formation of an acute auriculo-ventricular angle or ledge, that curves round but does not quite encircle this aperture. The ledge is most prominent where the expanding auricle bulges over the first part of the dorsal curvature, that is, over the dorsal wall of the proximal part of the bulbus, thus forming the bulbo-auricular groove (Text-fig. 9 *B* and Pl. 5, fig. 1, *B. Ag.*). On the posterior wall this constriction and its corresponding ledge reach the sides of the auriculo-ventricular ridge (plug), and, when the cardiac musculature appears (Stage 30), muscular bundles—musculature of the auricular canal—grow round this ledge and into the ridge posteriorly from either side, thus becoming continuous with the musculature of the developing interventricular septum. As development proceeds, the auriculo-ventricular opening becomes somewhat horseshoe shaped with the convexity anterior.

The bulbus also comes to be distinctly separated from the ventricle, partly by the disproportion of their rates of expansion, and partly by the increasingly abrupt curve with which the heart is bent on itself in this region. No valvular structure, apart from the spiral fold, appears in the aperture between the bulbus and the ventricle during any period of development. The bulbo-ventricular opening is, from the

first, situated directly in front of the auriculo-ventricular opening, and this relationship is permanent throughout development.

Septa.—While these changes have been taking place in the various chambers, defining them externally and internally from one another, localised cellular proliferations occur that give rise to the various septa of the adult heart. The first of these structures to appear (Stage 27)—the auriculo-ventri-

TEXT-FIG. 14.



Sagittal section through the heart at Stage 30. *A.* Auricle. *A. C.* Auricular canal. *av. r.* The auriculo-ventricular ridge. *B.* Bulbus cordis, with left ventral aorta above. *ph.* Endodermal pharyngeal rudiment. *ph. s.* Pharyngeal sheath continuous with *av. r.* *S. V.* Sinus venosus. *V.* Ventriele.

cular ridge—has already been partly described (p. 84) : it now remains to complete that description and to consider with it the development of the inter-auricular and interventricular septa, as well as, to a certain extent, that of the pulmonary vein. The auriculo-ventricular ridge is intimately related to all of these important structures, forming, as it were, their common point of convergence.

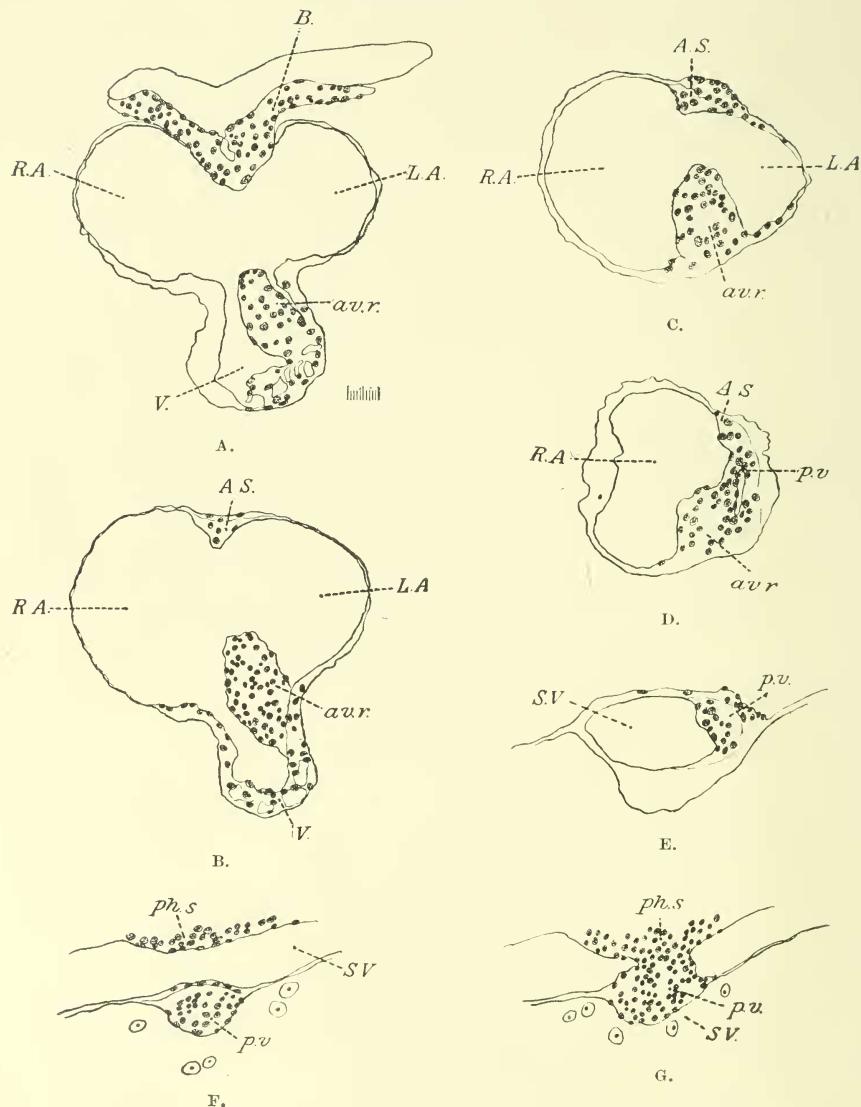
Pulmonary Fold.—The close relationship of the two

ends of the primitive heart-tube to the pharyngeal rudiment will be recalled.

The pharyngeal rudiment (Text-fig. 14, *ph.*) extends dorsally across the narrow pericardiac cavity, and, with its sheath, remains for some time closely applied to the sinus venosus behind the pericardium (Text-fig. 14, *S. V.*). When the cellular proliferation that gives rise to the auriculo-ventricular ridge occurs, its cells are continuous with those of the pharyngeal sheath along the left sinu-auricular angle (Text-fig. 15, *av. r.* and *ph.s.*).

A little later, about Stage 31, the pharynx becomes split off from the dorsal surface of the anterior part of the sinus, but this split occurs dorsal to a little column of cells (Text-fig. 15 *E*, *F* and *G*, *p.v.*) lying obliquely across the roof of the sinus, and arching down anteriorly across its left wall, where it is continuous with the auriculo-ventricular ridge and the interauricular septum (Text-fig. 15 *D* and *E*, *p.v.*). The splitting-off process occurs gradually from before backwards synchronously with the development of the pharynx and lung. Posteriorly, the little column of cells remains continuous with the ventral surface of the pharyngeal and lung rudiments (Text-fig. 15 *G*, *ph.s.*). Finally, it becomes the scaffolding along which the common pulmonary vein crosses the roof of the sinus venosus, and arches ventrally and to the left to reach the auricle from the ventral surface of the lung (Stage 31). Once in the auricle the pulmonary vein opens through a slit in the left side of this little cell mass, dorsal to the auriculo-ventricular ridge, and the margins of the opening presently project a little, forming a hood-like fold (Text-fig. 17, *P. V.*). The pulmonary vein therefore develops in the left wall and roof of the sinus venosus, but later, owing to the expansion of the auricles and the rotation of the heart, its terminal portion comes to lie deeply between the two auricles (Text-fig. 13, *P. f.* and *P. V.*). The pulmonary fold, to which reference has been made in the account of the adult heart (Pl. 5, fig. 1, *P. f.*), is thus formed by the right wall of the terminal portion of the pulmonary vein that passes for-

TEXT-FIG. 15.



Serial sections (transverse) through the heart of *Lepidosiren* at Stage 31. A. Through the anterior part of the ventricle. Note continuity of the auriculo-ventricular ridge (*av.r.*) with the ventricular musculature. B. Through the posterior region of the ventricle. C. Through the auricles. D. Anterior to the

wards across the dorsal surface of the auriculo-ventricular plug into the auricular cavity. By the fusion of its anterior margin with the developing muscular trabeculae of the interauricular septum (Text-fig. 15 c and d, *A. S.*, *p. v.*) this fold comes to form part of that structure. With the development of the pulmonary vein the left auricle and ventricle expand rapidly, approximating more to the dimensions of the compartments on the right side of the heart.

Interauricular Septum.—Simultaneously with the appearance of the pulmonary fold (Stage 31), a little growth of the endothelium of the auricular roof takes place across that part of it that may be said to be pinched in the narrow space between the bulbus cordis and the sinus venosus. The little endothelial fold (Text-fig. 15b, *A. S.*), the rudiment of the interauricular septum, arches across from the posterior wall of the bulbus to the anterior termination of the rudimentary pulmonary fold and the auriculo-ventricular ridge, and there fuses with them (Text-fig. 15a, b, c and d, *A. S.*), thus in its turn also coming into relation with the auriculo-ventricular ridge. Later, fine muscular strands develop in and about this little septum, forming an irregular meshwork of fibres placed more or less parallel to the long axis of the heart, but it does not appear to attain to any marked degree of development till after the adult stages are reached.

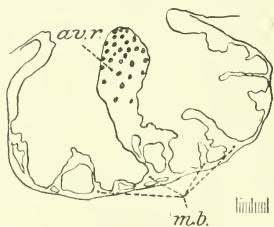
The situation and development of the interauricular septum as well as its relations to the auriculo-ventricular ridge (plug) are identical with those of the similar septum in Urodeles

sinu-auricular junction. The inter-auricular septum (*A. S.*), the wall of the pulmonary vein (*p. v.*) and the auriculo-ventricular ridge (*av. r.*) are all three continuous in this section. *E.* Posterior to the sinu-auricular junction. *F.* Through the sinus venosus posterior to fig. *E.* *G.* Through the sinus venosus posterior to fig. *F.* Note continuity at this point of the column of cells (*p. v.*) on the dorsal wall of the sinus in which the pulmonary vein will develop, with the tissue of the pharyngeal and lung sheath (*ph. s.*). *A. S.* Inter-auricular septum. *av. r.* Auriculo-ventricular ridge. *B.* Bulbus. *L. A.* Left auricle. *p. v.* Column of cells situated anteriorly on the left and posteriorly on the dorsal wall of the sinus venosus, in which the pulmonary vein will develop. *ph. s.* Pharyngeal sheath. *R. A.* Right auricle. *S. V.* Sinus venosus. *V.* Ventricle.

(12), where the posterior (dorsal) auriculo-ventricular pocket valve is homologous with the auriculo-ventricular plug of *Lepidosiren* (vide infra).

Interventricular Septum.—Meanwhile the interventricular septum and musculature are also appearing (Stage 30). Little subendothelial proliferations occur (Text-figs. 11 and 16, *av. r.*), connected with the tip of the auriculo-ventricular ridge, along the posterior (dorsal) and ventral walls of the ventricle somewhat to the left side. Almost immediately, however, other little muscular buds appear on the lateral walls as well (Text-fig. 16, *m. b.*).

TEXT-FIG. 16.



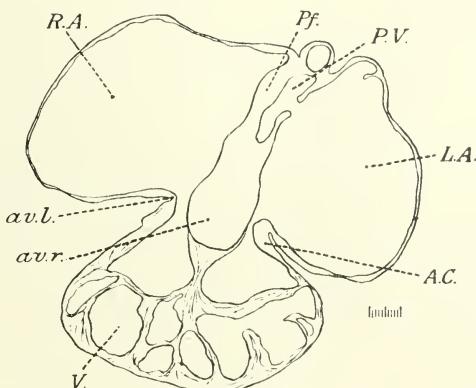
Section through the ventricle at Stage 31 showing buds of muscular tissue projecting into the ventricle. *av. r.* Auriculo-ventricular ridge. *m. b.* Muscle buds.

The last mentioned buds that are not from the first continuous with the auriculo-ventricular ridge project into the lumen of the ventricle, and as their somewhat club-shaped tips converge, sooner or later neighbouring buds coalesce, forming irregular arches and meshes which all again converge on the central "point d'appui" formed by the tip of the auriculo-ventricular ridge as it appears in the auriculo-ventricular aperture (Text-fig. 17).

These converging arches thus form trabeculæ that sweep on either side, from the posterior (dorsal) rim of the auriculo-ventricular aperture on to its lateral margins, and, mesially on to the anterior (ventral) margin of the bulbo-ventricular aperture. As the two apertures are situated antero-posteriorly,

so also are the more prominent, more mesially situated trabeculæ. Thus the interventricular septum is formed by the convergence of numerous muscular trabeculæ, from the floor and sides of the ventricle, upon the auriculo-ventricular plug. With the further growth of the heart and the elongation and expansion of the ventricles in a caudal direction, the radiating meshwork of muscular bands becomes more complicated and denser (Text-fig. 18, *V. S.*), as well as more

TEXT-FIG. 17.



Section through the heart at Stage 32. *A. C.* Auricular canal musculature. *a. v. l.* Auriculo-ventricular ledge. *av. r.* Auriculo-ventricular ridge (plug) in auriculo-ventricular opening continuous dorsally with the pulmonary fold and ventrally with the ventricular musculature. *L. A.* Left auricle. *P. f.* Pulmonary fold. *P. V.* Opening of pulmonary vein. *R. A.* Right auricle. *V.* Ventricle.

drawn out, until finally the septum acquires the solid character of the adult condition. As this ventricular increase in size is a matter of peripheral expansion, the right and left ventricles are formed, not so much by the upgrowth of the septum as by the expansion backwards of the ventricles on either side of it. The somewhat unequal division of the ventricular cavity into a larger right and smaller left compartment—due partly to the left-sided development of the

septum (Text-fig. 15 *a*, *b*, *c*, *d*, *av. r.*), partly to the comparatively late development of the pulmonary vein—is maintained throughout, though in the adult the disparity is very slight.

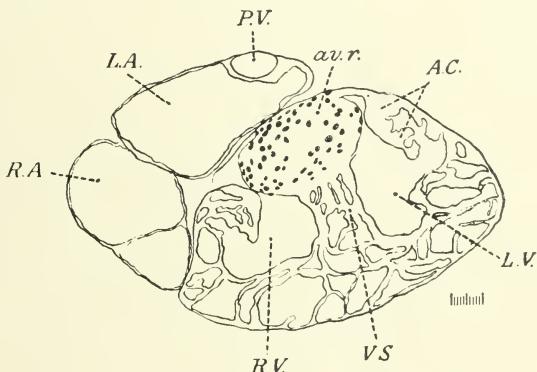
The interventricular septum in *Lepidosiren* would thus appear to be homologous with the incomplete posterior ventricular septum of *Lacerta*, and therefore also with the posterior muscular part of the complete interventricular septum of the *Alligator* or *Crocodile* (9).

Musculature of the Heart.—From the first the dense musculature and comparatively rigid walls of the auricular canal and proximal part of the *bulbus cordis* form a marked contrast to the rapid peripheral expansion and loose trabecular meshwork that characterise the ventricular and auricular chambers of the heart. As the ventricle expands its comparatively thin walls bulge round the comparatively rigid auricular canal and *bulbus cordis* respectively. The result at the auriculo-ventricular aperture is that the auricular canal has the appearance of being invaginated into the ventricle; really the ventricle has grown up round it. This brings the musculature of the auricular canal into direct relation with the posterior trabeculae of the developing interventricular septum posteriorly, and laterally with the endocardial surface of the ventricular musculature round the periphery of the auriculo-ventricular opening (Text-fig. 18, *A*, *C*). Anteriorly, the auricular canal comes directly in contact with the posterior wall of the proximal part of the *bulbus* at the *bulbo-auricular* fold (Text-fig. 9 *b*, *B. Ag.*) and the musculature of these two parts is continuous round it. On the auricular side the musculature of the auricular canal tapers off imperceptibly into that of the auricles (Text-fig. 17, *A. C.*). At the *bulbo-ventricular* aperture the ventricle bulges laterally and anteriorly round the proximal part of the *bulbus*, so that it also projects somewhat into the ventricle, but here the process appears to be more strictly a folding between the two divisions of the heart, and the ventricular and bulbar musculatures pass into one another round the edge of the fold. The muscula-

ture of the second and third parts of the bulbus is very poorly developed.

The relations in *Lepidosiren* of the developing ventricular musculature to the short auricular canal and the auriculo-ventricular ridge (plug) situated in that canal, resemble closely those of the ventricular musculature to the posterior (dorsal) auriculo-ventricular pocket valve in the elasmobranch (12). In *Lepidosiren*, however, the auriculo-ventricular ridge does not become hollowed out into a typical

TEXT-FIG. 18.



Horizontal section through the heart at Stage 32. *A. C.* Musculature of auricular canal continuous with endocardial surface of the ventricle. *av. r.* Auriculo-ventricular ridge (plug). *L. A.* Left auricle. *L. V.* Left ventricle. *P. V.* Pulmonary vein. *R. A.* Right auricle. *R. V.* Right ventricle. *V. S.* Interventricular septum.

pocket valve, and its muscular connections with the ventricular wall form the septum of that compartment of the heart.

Auriculo-ventricular Plug.—With the appearance of muscular fibres in the ventricle, the development of the interventricular septum and the definition of the auriculo-ventricular aperture, the auriculo-ventricular ridge becomes greatly thickened in its portion immediately dorsal to the auriculo-ventricular opening till it assumes the button shape that distinguishes its final form and adapts it admirably for

closing the auriculo-ventricular aperture. (Compare Text-figs. 17 and 18, *av. r.*)

Finally, the cellular matrix of which this structure is composed now develops into the cartilaginous tissue that gives it its characteristic consistency.

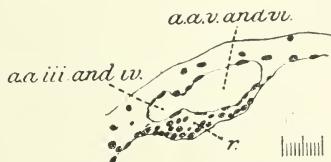
This auriculo-ventricular plug, therefore, originates in a little cellular proliferation at the left sinu-auricular margin, It extends along the short posterior auricular wall and lies in the auricular canal, projecting a little into the ventricular part of the heart. It is intimately related to the interven-tricular and interauricular septa, as well as to the pulmonary fold; throughout it is in proximity to the sinu-auricular opening and itself occupies the auriculo-ventricular aperture, while its actual area of attachment to the heart wall is the only representative in the adult *Lepidosiren* of the pos-terior auricular wall of the embryonic heart. The origin and situation of this plug would point to its homology with the posterior (dorsal) pocket valve of the auricular canal in elas-mobranchs; in *Lepidosiren*, however, there is at no time any trace of an anterior (ventral) valve. Again, its relations to the posterior (dorsal) arch of the interauricular septum and to the opening of the pulmonary vein point to its homology also with the posterior (dorsal) auriculo-ventricular endocardial cushion of the urodele (12). Thus the auriculo-ventricular plug in *Lepidosiren* may be regarded as a modified auriculo-ventricular pocket valve. Boas (2) suggests that the auriculo-ventricular plug of *Ceratodus*, which is a structure similar in position and general relations to that of *Lepidosiren*, arises from the fusion of the posterior (dorsal) valves of the approximated sinu-auricular and auriculo-ventricular openings, and compares the heart of *Ceratodus* with that of *Lepidosteus*, where these two-sets of valves are comparatively wide apart and quite distinct. As has been shown, the development of the auriculo-ventricular ridge in *Lepidosiren* distinctly supports this suggestion. The ridge appears first at the sinu-auricular junction and extends uninterruptedly along

the comparatively very short posterior auricular wall to the auriculo-ventricular junction.

Septa of the *Bulbus Cordis*.—At Stage 30 a thickening (Text-fig. 19, *r.*) is present on the ventral wall of each lateral ventral aorta, extending from a point between the origins of the common stems of the two anterior (third and fourth, Text-fig. 19, *a. a. III and IV*) and the two posterior (fifth and sixth, Text-fig. 19, *a. a. V and VI*) afferent vessels, to the distal end of the *bulbus cordis*.

In the *bulbus* itself, these ridges (*B. R. 1.* and *B. R. 3.*) extend along the lateral walls towards its proximal end

TEXT-FIG. 19.



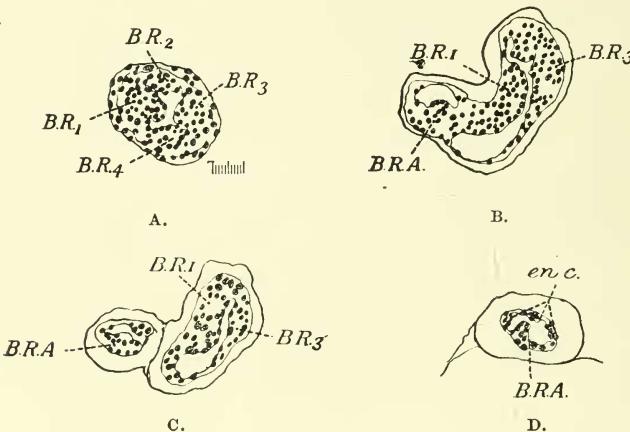
Section at Stage 30 transverse to the right ventral aorta at the point of divergence of the common stem of the third and fourth from that of the fifth and sixth afferent aortic vessels.
a. a. III and IV. Common stem of third and fourth aortic arches.
a. a. V and VI. Common stem of fifth and sixth aortic arches.
r. Ridge of thickening on ventral wall between the two vessel stems.

(Text-fig. 9c, *B. R. 1* and *B. R. 3*). The right ridge (*B. R. 1*) extends as far as the distal end of the proximal part of the *bulbus*, where it tapers off and is lost; the left ridge (*B. R. 3*) extends only about a third of the way along the left wall of the *bulbus*. In the proximal part of the *bulbus* a ridge (*B. R. A.*) also appears at the same time on the anterior (ventral in the adult) wall (Stage 31, Text-fig. 20B, c and d, *B. R. A.*).

Presently, about Stage 32, a general cellular proliferation occurs round the circumference of the whole length of the *bulbus*—except on the expanded middle part—which results at its distal end in the temporary appearance of two additional ridges (fig. 20A, *B. R. 2* and *B. R. 4*) between the

first and third ridges, while in the proximal part three little cushions (fig. 20D, *en. c.*) appears on the posterior (dorsal) and lateral walls. Ridge 4 tends to become fused with ridge 1 and in two specimens could only be traced at intervals, the walls of the bulbus being occupied by the ridges 1, 2 and 3. The additional second and fourth ridges disappear with the general flattening of the bulbar lining that soon follows, but the little secondary cushions in the proximal part remain and

TEXT-FIG. 20.



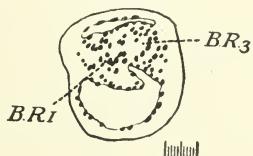
Serial sections (transverse) through the heart of *Lepidosiren* at Stage 34. A. Through the distal end of the bulbus cordis. B. Through the transverse segment of the bulbus. Note the continuity of the ridge (B. R. A.) on the anterior (ventral) wall of the proximal segment of the bulbus, along the transverse segment with the right bulbus ridge (B. R. 1). C. Through the posterior part of the transverse segment of the bulbus. D. Through the proximal end of the proximal segment of the bulbus. B. R. 1. Right bulbus ridge. B. R. 2. Posterior temporary ridge. B. R. 3. Left bulbus ridge. B. R. 4. anterior temporary ridge. B. R. A. Ridge on the anterior (ventral) wall of the proximal segment of the bulbus. *en. c.* En docardial cushions of rudimentary pocket-valves.

are visible in the adult, where they form the rudimentary pocket-valves. The right and left ridges (B. R. 1 and B. R. 3) and the A ridge persist as the septa of the adult bulbus, ridges 1 and A forming together the spiral valve.

At the junction of the lateral ventral aortæ to form the extremely short ventral aorta, the free edges of the ridges on their ventral—posterior in the adult—walls (Text-fig. 19, *r.*) fuse in the middle line: the horizontal partition so formed unites at its distal extremity with the dorsal wall of the aorta, thus cutting off the fifth and sixth from the fourth and third pairs of afferent aortic vessels (Text-fig. 21, *B. R. 1*, *B. R. 3*).

Meanwhile the rotation and asymmetrical bulging of the bulbus cordis already described have taken place, with the result that the consequent kinking towards the left between its proximal and middle (transverse) segments brings the projecting free margin of the proximal extremity of the 1 ridge,

TEXT-FIG. 21.



Transverse section at Stage 36 through the distal end of the bulbus cordis (ventral) aorta showing fusion of the right and left ridges or valves. *B. R. 1.* Right ridge. *B. R. 3.* Left ridge.

and the distal extremity of the left side of the *A* ridge, into close proximity round the rim of the kink between these two segments (Text-figs. 12 *a*, *b*, and *c*, and 20 *b*, *B. R. 1*, and *B. R. A.*) of the bulbus.

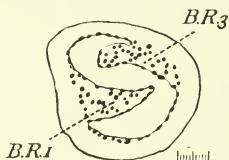
Consequently the two ridges fuse and form the spiral valve. This spiral valve therefore arises in *Lepidosiren* discontinuously in two portions, one, namely, belonging to the ventral wall of the proximal segment of the bulbus (*A* ridge) and one belonging originally to the right wall (*B. R. 1* ridge) of the distal and middle segments. It has already been shown, however, how, in the process of development, the right wall of the middle segment was carried transversely and somewhat posteriorly and with it the valve situated on its endothelial surface. The two portions of the spiral valve,

therefore, finally come in contact with one another round the left margin of the constriction that demarcates the proximal from the middle segment. Finally, (in the adult horizontal position of the heart) the free inner borders of the first and third septa incline towards one another in the lumen of the bulbus, and the former becomes concave on its dorsal and the latter on its ventral surface (Text-fig. 22, *B.R. 1* and *B.R. 3*.).

In the transverse part of the bulbus, the transverse continuation of septum 1 maintains this concavity, which, however, in this region is directed posteriorly (Pl. 5, figs. 1, 2, and 4, *Sp. V.t.*).

The chief interest in tracing the development of the bulbus

TEXT-FIG. 22.



Transverse section through the distal segment of the bulbus cordis at Stage 37. *B.R. 1*. Right bulbus ridge (spiral valve). *B.R. 3*. Left bulbus ridge (left longitudinal valve.)

cordis in *Lepidosiren* is the information so obtained concerning the formation of the spiral valve. If the foregoing observations are correct, then—at least in *Lepidosiren*—the bulbus valve owes its spiral form to the process of kinking and asymmetrical expansion of an elongated but originally straight bulbus, and not to any twisting or counter-twisting of that segment of the heart. Boas (2) comments upon the difficulty of believing that any twisting of the bulbus (conus) occurs in *Ceratodus*, but having only an adult specimen at his disposal for examination cannot suggest any other more satisfactory explanation for the presence of a spiral valve. It is of interest to note how closely the above account of the development of the bulbus cordis and its associated endothelial structures agrees with that given by Langer (16) and Greil (9) for amphibians and reptiles.

When they first appear at either end of the heart, the non-muscular septa are formed by proliferations of the local mesenchyme cells, but as they grow proximally away from their points of origin into the heart itself, the endothelial cells appear to take a larger and larger part in their formation. It is extremely difficult to dogmatise, however, as to the exact derivation of these septal cells, as the mesenchyme and endothelial elements much resemble one another, but undoubtedly proliferation of the endothelial cells does occur at the proximal ends of the growing septa. The endothelial origin of the endocardial cushions in the elasmobranchs would point to the probability of a similar origin in *Lepidosiren*.

As far as any considerable changes in shape are concerned, the development of the heart may now be considered to be complete. The only change still taking place is that the ventricular and auricular walls continue for a time to become increasingly muscular.

IV. DEVELOPMENT OF THE ARTERIES.

Aortic Arches.—The endothelial rudiments of the lateral ventral aortæ are present about Stage 24 (24 segments); they pass from the mesial heart rudiment between the parietal layer of the pericardium and the lateral expansions of the pharyngeal rudiment sharply outwards dorsally, and a little backwards to the sides of the head.

A little later, Stage 25, the rudiments of the four external gills appear on the dorso-lateral surfaces of the head, and the ventral aorta (Text-fig. 23 A, *V. A.*) on either side is prolonged outwards and dorsally to their bases, giving an afferent branch to each of the four posterior gill-rudiments, there being no afferent aortic branches to the first and second (mandibular and hyoid) arches. Correlated, however, with the flattening of the embryo and the extreme lateral position of the gill-rudiments at the sides of the neck, the origins of the four posterior aortic arches are fused together, one behind the other at the outer extremity of the paired ventral aorta

TEXT-FIG. 23.

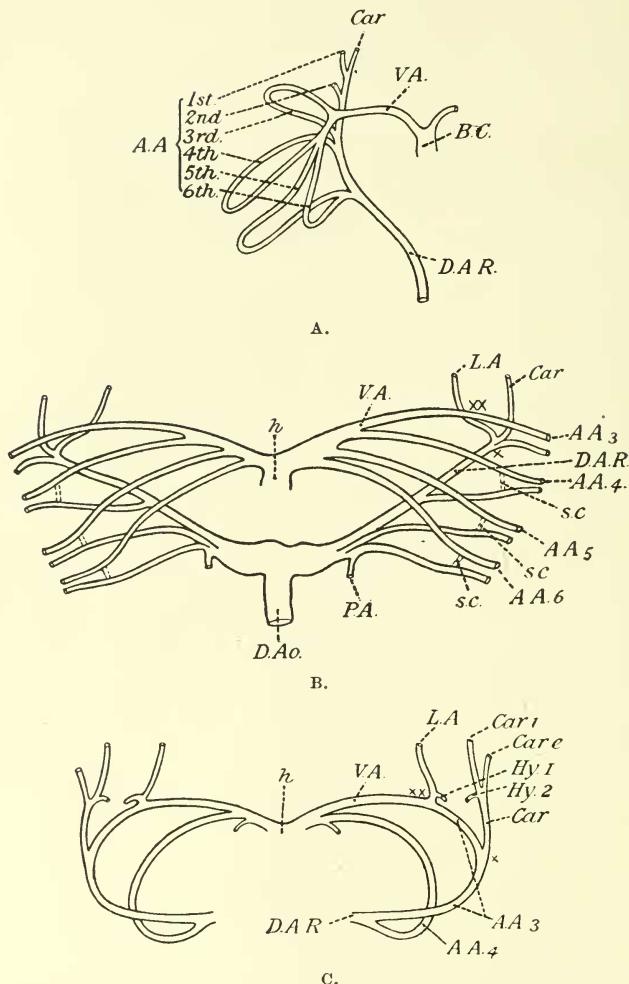


Diagram of the development of the aortic arches. Ventral view.

A. About Stage 26. B. About Stage 33-34. C. About Stage 35. A. A. The six aortic arches of which 1 and 2 are incomplete. B. C. Bulbus cordis. Car. Dorsal carotid artery, Car. e. External branch of carotid. Car. i. Internal branch of carotid. D. Ao. Dorsal aorta. D.A.R. Dorsal aortic root. h. Heart. Hy. 1. Branch to hyoidean hemibranch. Hy. 2. Hyoidean efferent artery. L. A. Lingual artery. P. A. Pulmonary artery. s. c. Short-circuiting channels between the afferent and efferent branchial vessels. V. A. Ventral aorta.

(Text-fig. 23 A, *A. A.*). These afferent branches are at first very short and each is continuous with an efferent branch that passes back along the gill, dorsal to the afferent vessel. Each efferent vessel in turn joins the dorsal aortic root (Text-fig. 23 A, *D. A. R.*), which passes from just in front of the mandibular arch, backwards and inwards towards the middle line, where ultimately it meets its fellow of the opposite side behind the heart in the region of the pronephros, forming the unpaired dorsal aorta. In the region of the mandibular and hyoid arches the dorsal aortic root receives a slender first and second efferent aortic vessel (Text-fig. 23 A, *A. A. 1* and *2*). The present observer has not been able to determine any connection between the lateral ventral aorta and these two vessels, though possibly an exceedingly fine communication may exist for a time. The ventral end of the first aortic vessel is prolonged downwards and inwards along the outer side of the mandibular arch over the ventral surface of the pericardium and terminates in the region of the cement organ. With the commencing atrophy of that organ, the little vessel breaks up and disappears about Stages 33-34. The second incomplete aortic arch, which is even more insignificant than the first, disappears still earlier.

The four posterior external gills grow out rapidly into conspicuous projecting structures on the sides of the head, and give off long feathery filaments through which the branchial vessels pass, forming a fine capillary loop in each. Subsequently with the development of the opercula, the external gills gradually disappear, and, with the establishment of the mouth-cavity and the definition of the gill-clefts, each pair of vessels becomes continuous round its respective branchial arch by means of a new short-circuiting vascular channel that develops between the dorsal and ventral (efferent and afferent) vessels (Stages 34-38, Text-fig. 23 B, *s. c.*). These new channels—where the fourth, fifth and sixth pairs of aortic arches are concerned—appear as little widening chinks between the respective vessels, but unlike what happens in urodeles (18), cannot be said to develop either from afferent

to efferent, or efferent to afferent sides of the arches. The short-circuiting channels of the sixth aortic arches do not expand so markedly as do those of the fifth, fourth and third. The sixth arches themselves dwindle in size, the fifth aortic arches now bringing the main supply of blood to the pulmonary vessels. The pulmonary vessels in turn, owing to the diminished calibre of the sixth aortic arches, finally have the appearance of arising directly from the dorsal aortic roots instead of from the arches themselves (Text-fig. 2, *P. A.*).

The short-circuiting of the third aortic or first branchial arches occurs somewhat differently and must be considered separately. About Stage 31 a new vascular channel appears at the junction of the third efferent aortic vessel with the dorsal aorta (Text-fig. 23 *B*, *L. A.*, *x.*), and passing dorsally to and obliquely across the afferent branch of the third aortic arch in the first branchial arch, reaches the root of the tongue, and is prolonged forwards along the side of that organ (Text-fig. 23 *B*, *L. A.*) as the lingual artery. Later this new vessel fuses with the third aortic arch just where that vessel passes into the first branchial arch at the root of the tongue (Text-fig. 23 *B*, *xx.*), that is to say, just at the outer termination of the lateral ventral aorta. The third aortic arch now disappears between this point of fusion (Text-fig. 23 *B*, *xx.*), and the point of origin of the new artery from the dorsal aorta (Text-fig. 23 *B*, *x.*), so that the new vessel forms the short-circuiting channel for the third aortic arch (compare figs. 23 *B* and 23 *C*, *L. A.* *xx.* and *x.*).

This apparent origin of the lingual artery from the dorsal aortic root must be regarded as a secondary condition due probably to the precocious development of the short-circuiting vessel of the third aortic arch. It is a temporary condition only, and with the formation of the short circuit a small vessel develops (Stage 38) at the junction of the lingual artery with the ventral aorta (Text-fig. 23 *C*, *Hy. 1.*), and passes outwards and backwards along a little gill-rudiment—hyoidean hemibranch—that appears (Stage 38) in the angle between the first branchial arch and the lateral wall of the mouth. This

little gill is drained by a tiny efferent vessel which joins the dorsal carotid artery just at the point of divergence of its internal and external branches (Text-fig. 23 c, *Hy.* 2).

The presence primarily of six aortic arches, of which the two first are incomplete, having no connection with the ventral aortæ, may be compared with the early condition described for *Lepidosteus* (19). The later development of the four posterior aortic arches, however, with the formation of the lingual artery and the disappearance of the first and second arches, closely resembles the condition in *Urodeles*, and the lingual and dorsal carotid vessels of *Lepidosiren* are homologous with the external and internal carotids respectively of the former (3).

Dorsal and Ventral Aortæ.—The dorsal aortic roots, formed by the efferent branchial vessels on either side, join below the notochord in the region of the pronephric glomeruli to form the dorsal aorta (Stage 25, forty-seven segments). Immediately before doing so they give a branch to each glomerulus. The dorsal aorta is now present throughout the greater length of the embryo; quite anteriorly it is a patent dilated vessel, but further back it is a flattened tube, while quite posteriorly it is merely a little rod of yolk cells that are beginning to vacuolate. For a short period (Stage 26) the aorta bifurcates posteriorly and communicates with the posterior terminations of the posterior cardinal veins, while a little later (Stage 29) it extends backwards and anastomoses round the post-anal gut with the caudal vein. (A similar stage is recorded in the development of *Polypterus* (15)). These connections are soon lost, however, and finally the caudal aorta lies in the haemal canal immediately dorsal to the caudal vein, owing to the post-anal gut having disappeared. Anteriorly with the absorption of the yolk and the general development of the embryo, the junction of the dorsal aortic roots gradually occurs further forward nearer the heart, so that finally the unpaired dorsal aorta extends some little distance in front of the pronephric region, while the length of the dorsal aortic roots is proportionately

shortened. Meanwhile, as the adult condition is attained, the long axis of the ventral aorta becomes horizontal.

Carotid Arteries.—The carotid arteries appear early as prolongations forwards of the dorsal aortic roots passing ventral to the anterior cardinal veins (Text-fig. 23 *a*, *Car.*). As development proceeds they come to lie below the otocysts, and give off an external branch which is distributed with the developing trigeminal nerve (Text-fig. 23 *c*, *Car. e.*), after which they pass sharply inwards to the ventro-lateral surfaces of the brain. An anastomosis occurs between the two internal carotid vessels below the hind brain, and then, after passing forwards a little, they anastomose on each side with the vertebro-cerebral artery (see below) round the hypophysis, and are then distributed to the mid- and fore-brains.

Vertebro-cerebral Arteries.—About Stage 28 two little vessels appear on the dorsal surface of the dorsal aortic roots passing to the ventral surface of the posterior part of the hind brain. These vessels, the vertebral arteries, are prolonged along the ventral surface of the hind-brain and anastomose at intervals along their course (Text-fig. 2, *V.C.A.*). Finally they reach well on to the dorsum of the hypophysis, forming a single median trunk, and then, separating again practically at right angles, curve round on either side and join the internal carotid vessels on the sides of the mid-brain. A little later each develops at its point of entry to the hind-brain a posterior or vertebral branch, that is continued backwards along the ventral surface of the spinal cord as far back as the origins of the first pair of segmental arteries posterior to the subclavian vessels. Posterior to this, each pair of segmental arteries supplies a twig to these vertebral vessels. Homologous vessels are described for *Lacerta* and *Tropidonotus* (1).

Cœliac Artery.—The arteries to the pronephric glomeruli appear on the formation of the dorsal aorta (Stages 24-25). They enter the glomeruli dorsally, and after winding throughout their length, leave them ventrally and disappear among

the pronephric tubules, where it is impossible to trace them among the sinuses of those structures. It is possible that the glomerular arteries may establish connections with the vitelline meshwork for a time, through the pronephric sinuses. At Stages 31-32 the developing liver comes in contact with the ventral surface of the right glomerulus and pronephric tubules and a small artery passes from the tip of the glomerulus along the right outer angle of the liver, and, crossing ventral to that organ, reaches the right wall of the developing gut. At Stage 36 with the atrophy of the glomeruli and pronephric tubules, the left glomerular artery disappears, but the right artery persists as the cœliac artery. In *Lepidosiren* apparently there is only one vessel to each pronephric glomerulus, and the cœliac artery receives no branches either directly or indirectly from the aorta, and only anastomoses with the anterior mesenteric artery in the walls of the intestine. There is no evidence of any shifting of the root of this vessel during development.

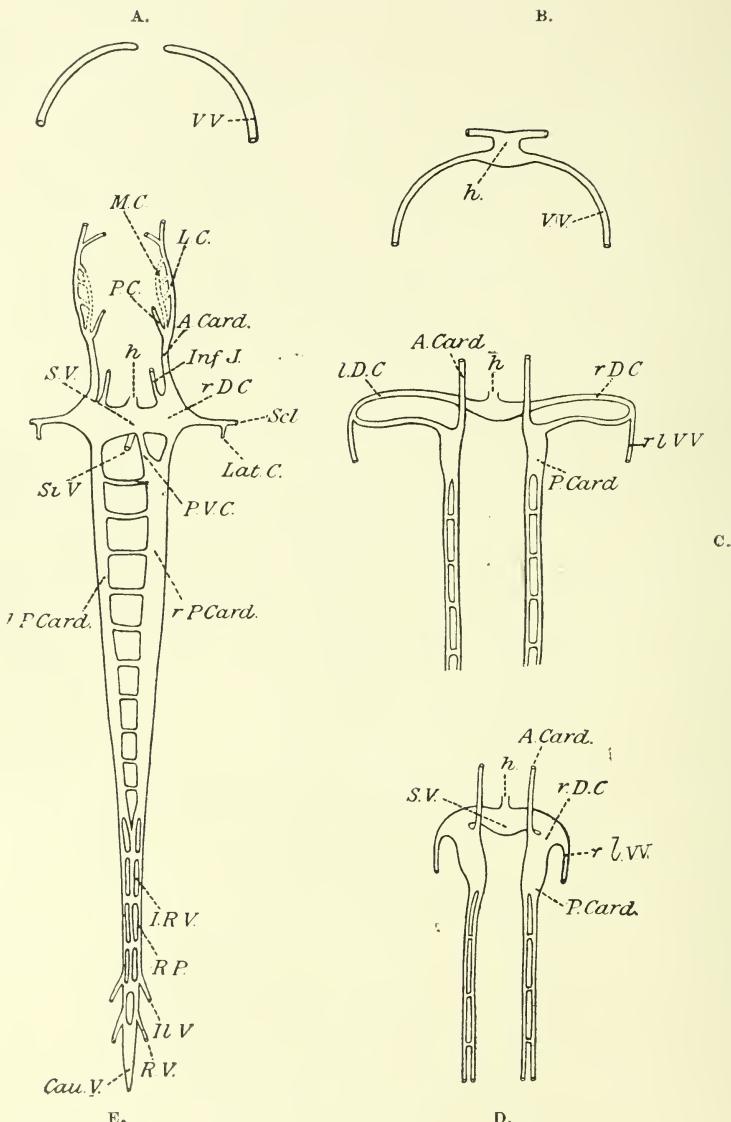
Pulmonary Arteries.—The pulmonary arteries appear about Stage 31 +, arising from the sixth aortic arch on either side. When the sixth aortic arch dwindle in size, as already described, the pulmonary artery comes to open from the common stem of the fifth and sixth aortic arches, receiving its main blood-supply from the fifth. With the rotation of the lungs, the right pulmonary artery comes to be distributed to the dorsal and the left to the ventral surfaces of the lungs.

The segmental aortic vessels from which the mesonephros receives its arterial blood-supply appear about Stages 31, 32, as do also the subclavian, pelvic and mesenteric arteries.

V. DEVELOPMENT OF THE VEINS.

Ductus Cuvieri.—At Stage 24 + (twenty-four segments) the endothelial rudiments of the vitelline veins extend, posterior to the pericardium, one on either side, across the anterior surface of the yolk, outwards and somewhat posteriorly (Text-fig. 24 a, *V. V.*).

TEXT-FIG. 24.



Diagrams of developing venous system, dorsal view. A. Diagram of developing vitelline veins. B. Diagram of junction of vitelline veins and formation of the heart. C. and D. Diagram

A little later (Stage 24) the inner ventral ends of these endothelial vessels fuse and form the posterior part of the primitive heart-tube from which the sinus venosus is developed (Text-fig. 24 b, *V. V.*).

The peripheral ends of the vitelline veins communicate with the blood-spaces appearing on the lateral surfaces of the yolk (Stages 24-25), and simultaneously the anterior cardinal veins appear in the lateral regions of the head, passing backwards dorsal to the developing branchial vessels as far as the inner margins of the anterior ends of the developing pronephric sinuses (posterior cardinal veins) on either side. The pronephric sinuses in turn are, as in *Polypterus* (15), connected for a time at intervals along their outer margins with the vitelline meshwork; and also as in *Polypterus* and *Belone* (22) the most anterior of these connections curves outwards, downwards and forwards, communicating directly with the vitelline vein going to the heart and thus forming a venous arch over the lateral surface of the yolk. These venous arches, ducts of Cuvier, each receive for a time a main lateral vitelline vein from the lateral surface of the yolk, both of which vessels become modified later on with the development of the liver and sub-intestinal vein (Text-fig. 24 c, *r. D. C.* and *l. D. C.*). As the yolk is absorbed the ducts of Cuvier finally become much shortened, forming straight lateral trunks on either side of the heart, and giving rise to the sinus venosus at their point of junction behind it. With the appearance of blood-spaces in the liver (Stages 30-31) the ducts of Cuvier become much

of developing cardinal veins. E. Diagram of venous system.
A. Card. Anterior cardinal. *Cau. V.* Caudal vein. *h.* Heart
Il. V. Iliac vein. *Inf. J.* Inferior jugular vein. *I.R.V.* Inter-renal
 vein. *L. C.* Lateral cephalic section of anterior cardinal. *Lat.*
C. Lateral cutaneous vein. *l. D. C.* Left ductus Cuvieri.
l. P. Card. Left posterior cardinal. *M. C.* Obliterating median
 cephalic section of anterior cardinal vein. *P. Card.* Posterior
 cardinal vein. *P. C.* Posterior cerebral. *P. V. C.* Posterior
 vena cava. *R. V.* Rectal vein. *R. P.* Renal portal vein. *r. P.*
Card. Right posterior cardinal vein. *r. D. C.* Right ductus
 Cuvieri. *r. l. V. V.* Right lateral vitelline vein. *Scl.* Sub-
 clavian. *Si. V.* Subintestinal vein. *S. V.* Sinus venosus. *V. V.*
 Vitelline veins.

expanded, and each forms a great venous channel extending transversely across the upper part of the anterior surface of the liver, into the outer ends of which the anterior and posterior cardinal veins open at right angles opposite one another on either side (Text-fig. 24 *D*, *r. D. C.*).

The posterior cardinal vein (pronephric sinuses) thus come into close relationship with the sinuses in the liver. The venous channels developing in the liver become concentrated towards the right in the neighbourhood of the sinus venosus and form a wide vessel opening into it ventrally (Stages 31-32).

Posterior Cardinal Veins and Caudal Veins.—With the development of the pronephric tubules and archinephric ducts, blood-spaces appear round them, foreshadowing the two posterior cardinal veins (Text-fig. 24 *c* and *d*, *P. Card.*). These spaces develop rapidly into considerable sinuses at the anterior ends of the tubules and communicate with the anterior cardinal veins, forming the ducts of Cuvier as described. Posteriorly these sinuses are continued along each archinephric duct as two vessel-rudiments, one on the inner dorsal and one on the outer ventral surface, which are connected round the duct by frequent anastomoses, forming the posterior cardinal veins. The posterior cardinal veins extend along the archinephric ducts to their terminations on the sides of the cloaca (Stage 24), and, passing a little ventrally and forwards, are then continuous with the blood-spaces appearing on the ventral surface of the yolk, joining the precloacal subintestinal vein, which at this stage is still extremely short. An anastomosis occurs between the posterior termination of the aorta and the posterior cardinal veins at Stage 27 (Text-fig. 25, *D. Ao.*; *P. Card.*), and the lateral trunks formed by the junction of these vessels (i. e. the posterior cardinal vein and the bifurcations of the aorta and subintestinal vein on either side) join almost immediately and form the short caudal vein ventral to the post-anal gut.

As the post-anal gut lengthens, the aorta and caudal vein

extend backwards, communicating round it by one or two vertical anastomoses (Stage 29). These post-anal vessels are remarkable for their width and form large vascular loops round the gut. With the development of the tail and the disappearance of the post-anal gut, the caudal vein lengthens and the hoop-like anastomoses with the aorta disappear, while the vein comes to lie immediately ventral to the aorta (Stage 31).¹ In the region of the cloaca, therefore, the caudal vein bifurcates to reach the posterior cardinal veins, which are joined in the same region by the bifurcations of

TEXT-FIG. 25.

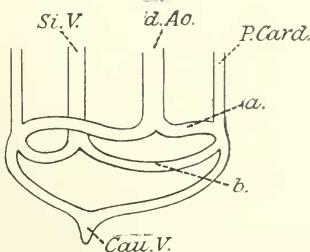


Diagram of anastomoses between the dorsal aorta and the posterior cardinal and subintestinal veins. *Cau. V.* Caudal vein. *D. Ao.* Dorsal aorta. *P. Card.* Posterior cardinal vein. *Si. V.* Subintestinal vein. *a.* The anastomosis between the dorsal aorta and the posterior cardinal vein. *b.* The anastomosis between the subintestinal and posterior cardinal veins.

the subintestinal vein. These latter vessels (the bifurcations of the subintestinal vein) presently lose their connections with the subintestinal vein and persist in the adult as the rectal veins (Text-fig. 24 E, *R. V.*). A little later (Stage 31+) the iliac veins (Text-fig. 24 E, *Il. V.*) open into the renal portal vessels a short distance in front of the cloaca.

Meanwhile, with the gradual absorption of the yolk, the archinephric ducts approach one another in the middle line, and, with the appearance of the mesonephros dorsal and

¹ A similar condition is described in the development of *Polypterus*. Kerr, J. Graham, "The Development of *Polypterus senegalus*, Cuv." The work of John Samuel Budgett, Cambridge, 1907.

immediately internal to them, the outer and inner channels of the posterior part of each posterior cardinal vein are separated to some extent. Later the inner trunks meet and fuse temporarily, forming a median interrenal vessel (Text-fig. 24 e, *I. R. V.*), while the outer trunks form the renal portal vessels (Text-fig. 24 e, *R. P.*). In front of the mesonephros the outer vascular channels disappear, becoming apparently fused with the inner channels. Numerous anastomoses occur between the inner and outer trunks through the substance of the mesonephros.

The development of the posterior cardinal veins up to this point thus closely resembles that of the same vessels in the Urodeles (11), with this difference, that in *Lepidosiren* the fusion of the two posterior cardinal veins across the middle line is only a temporary, not a permanent condition.

At the same time (Stage 31) changes occur in the posterior cardinal veins cranial to the mesonephros. The right posterior cardinal becomes the larger of the two vessels, and transverse anastomoses appear segmentally between them as far forwards as the region of the pronephric glomeruli (Text-fig. 24 e, *r.* and *l. P. Card.*). The main blood-stream is thus deflected to the right and a large new vascular channel appears in the mesentery of the liver. This new channel arises on the right at the level of the most anterior anastomosis between the posterior cardinal veins (Text-fig. 24 e, *P. V. C.*), and passes forwards in the triangle formed by the pronephros on the right, the lung rudiment on the left and the yolk and liver ventrally. Where it passes from the surface of the yolk on to that of the liver, the anterior termination of this vessel is continued into the wide channel formed by the liver sinuses and subintestinal vein and so enters the sinus venosus (Stage 31), while posteriorly it is in continuity with the wide trunk of the right posterior cardinal vein, thus forming the posterior vena cava. The front part of the posterior vena cava appears in the mesentery of the liver, on the ventral surface of the lung rudiment ventral to the common pulmonary vein. This close relationship is maintained throughout

development, the latter vessel resting on the dorsal surface of the former in the adult. The development of the posterior vena cava, as just described, is very similar to the condition in Urodeles (11), where the new vessel connects the fused portions of the posterior cardinal veins (which, however, separate again in *Lepidosiren*) directly with the heart through the liver.

As the lung and foregut extend backwards, they form a barrier between the left posterior cardinal vein and the posterior vena cava (right posterior cardinal), so that their transverse anastomoses gradually disappear from before backwards, even the fused portions of the posterior cardinal veins in the posterior mesonephric region (interrenal vein) are wedged apart again, and in the adult only one or two transverse anastomoses persist across the middle line towards the posterior end of the body (compare Text-figs. 24 E and 3). At the same time the two posterior cardinal vessels lose their connection with the renal portal vessels at the caudal extremity of the mesonephros, and no longer receive blood from the caudal vein. Finally, therefore, the main inner channels on the inner dorsal surfaces of the mesonephros are formed by the left posterior cardinal and the posterior vena cava (right posterior cardinal) respectively. With the atrophy of the pronephros the anterior part of the right posterior cardinal vein loses its connection with the posterior vena cava in the region of the pronephric glomerulus (compare Text-figs. 24 E and 3, *r. P. Card.*), and is represented in the adult by a short vessel that receives one or two small tributaries from the body-wall and a vein from the vertebral region, and joins the anterior cardinal vein to form the right duct of Cuvier. The left posterior vein persists as a long, somewhat slender trunk passing forwards from the left mesonephros between the intestine and the body-wall to the left duct of Cuvier (Text-figs. 24 E and 3, *l. P. Card.*).

Anterior Cardinal Veins.—The anterior cardinal veins appear early in the lateral regions of the head (Stage 25), arching backwards dorsal to the branchial vessels, and

communicating with the ducts of Cuvier at their junction with the pronephric sinuses (posterior cardinal veins, Text-figs. 24 c and d, *A. Card.*). The anterior ends of these vessels bifurcate in the region of the eye, one branch being superficial, and one, the anterior cerebral vein, passing deeply from the front part of the head. As they pass backwards the anterior cardinal veins lie ventral to the otocysts and then curve inwards internally to the posterior cranial nerves, and then outwards again a little to reach the pronephric sinuses. Presently, however, a new vessel appears on either side below and slightly external to the otocysts. This new vessel arises from the anterior cardinal vein immediately anterior to the ganglion of the seventh and eighth cranial nerves, and, passing immediately external to it, joins the anterior cardinal vein again between the eighth and ninth nerves (Stage 30). A little later (Stage 31) the outer vessel grows further back externally to the ninth nerve, and then joins the anterior cardinal vein between the ninth and tenth nerves, while finally (Stage 31+) it extends backwards external to the tenth nerve and joins the anterior cardinal vein behind it. Meanwhile, as each fresh segment of this lateral cephalic vessel develops, the corresponding stretch of anterior cardinal vein (median cephalic) disappears from before backwards (Text-fig. 24 e, *M. C.*). The posterior part of the third segment of the median cephalic persists, however, in the adult as a short wide vessel between the skull and muscles of the head, opening with the posterior cerebral vein from the interior of the skull, into the lateral cephalic vein behind the otocyst. Finally, the lateral cephalic vein passes below the otocyst and external to the cranial nerves, being continuous with the anterior cardinal vein in front of and behind them and forming to all appearances simply a portion of the anterior cardinal. In *Lepidosiren* therefore, while the main features of the development of the anterior cardinal veins are the same as for all vertebrates, the details tally closely with those given for the same vessels in *Tropidonotus* (10).

Posterior Cerebral Veins.—At Stage 28 a small vessel from the brain opens into each anterior cardinal vein some distance posterior to the otocysts. A little later (Stage 31+) the posterior anastomosis of the lateral cephalic vein with the anterior cardinal occurs just in this region, and, when the median cephalic part of the latter vessel atrophies, the cerebral vein (Text-fig. 24 e, *P. C.*) and the short persistent posterior part of the median cephalic open together into the lateral cephalic vein. This relationship persists in the adult, the cerebral vessel forming the posterior cerebral branch of the anterior cardinal vein.

Lateral Vitelline and Subintestinal Veins.—When the primitive vitelline veins become connected over the lateral surfaces of the yolk with the anterior and posterior cardinals so that they may now be termed the ducts of Cuvier (Text-fig. 24 c, *D. C.*), they also become connected with the general vitelline meshwork by means of two main lateral vessels one on either side (Text-fig. 24 c, *r. l. V. V.*). These lateral vitelline veins extend backwards and ventrally over the sides of the yolk towards the anus, their tributary vessels forming intricate anastomoses all over its surface: in the region of the anus they fuse and form the, at first extremely short, subintestinal vein (Text-fig. 26 a, *lat. V. V., Si. V.*).

A little later (Stage 32) three main vessels can be traced over the yolk towards the heart, viz. two lateral and one smaller median vessel (Text-fig. 26 b, *r. and l. lat. V. V., Si. V.*).

The appearance of this median vessel by short-circuiting through the network on the yolk, synchronises with the development of blood-sinuses in the liver (Stage 31), which form a wide vessel, opening ventrally into the sinus venosus on the right side. The median vitelline or subintestinal vein is continuous with the liver-sinuses over the antero-ventral surface of the yolk, the former channel thus obtaining access to the heart. With the further development of the embryo, and the definition of the liver and gut, the right lateral vitelline vein disappears, and the left vessel

TEXT-FIG. 26.

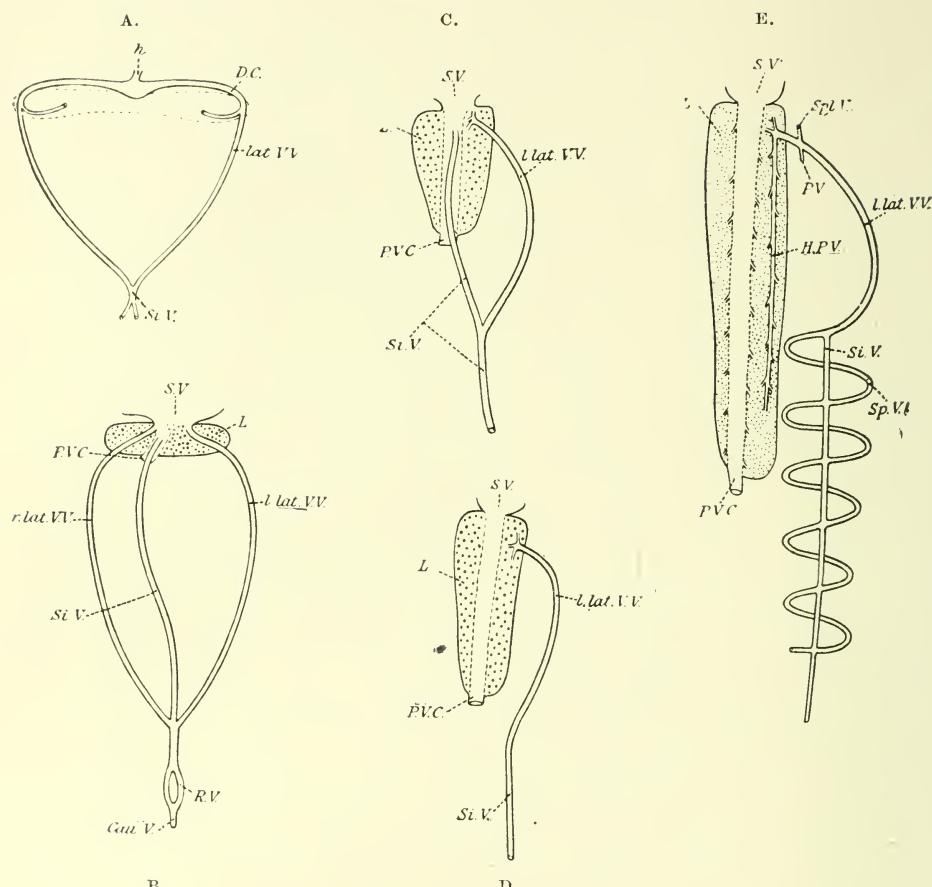


Diagram illustrating the development of the lateral vitelline and subintestinal veins and of the portal system. A. Diagram of lateral vitelline veins. The approximate site of appearance of the liver is indicated by the dotted line. B. C and D. Diagrams of lateral vitelline and subintestinal veins. E. Diagram of the portal system. *Can. V.* Caudal vein. *D. C.* Duct of Cuvier. *h.* Heart. *H. P. V.* Hepatic portal vessel. *L.* Liver. *lat. V. V.* Lateral vitelline vein. *P. V.* Pancreatic vein. *P. V. C.* Posterior vena cava. *r. and l. lat. V. V.* Right and left lateral vitelline vein. *R. V.* Rectal vein. *Si. V.* subintestinal vein. *Spl. V.* Splenic vein. *Sp. V.* Spiral vein. *S. V.* Sinus venosus.

loses its direct communication with the sinus venosus and breaks up into capillaries in the liver substance (Text-fig. 26 c, *l. lat. V. V.*).

At the same time the left lateral vitelline vein becomes connected with the venous spaces appearing in the spleen and pancreas, while it is still continuous round the dorsal wall and left side of the gut with the subintestinal vein. The anterior or hepatic segment of the subintestinal vein now disappears (Stage 35) as far back as its junction with the left vitelline vein, so that the hinder persistent part of the subintestinal vessel (Text-fig. 26 d, *Si. V.*) loses its direct connection with the liver and sinus venosus, which it now reaches by means of its anastomosis round the left side of the gut with the left vitelline vein (Text-fig. 26 d, *l. lat. V. V.*). The lateral vitelline vein arches round the gut parallel with the insertion of the spiral valve, and at its junction ventrally with the subintestinal vein a tributary vein (Text-fig. 26 e, *Sp. V.*) emerges on the opposite side of that vessel, and passing round the gut, follows the line of insertion of the spiral valve and fuses with the subintestinal vein at each point where it crosses the mid-ventral line.

This vein of the spiral valve therefore forms a series of diminishing spiral coils that are united ventrally by the subintestinal vein (Text-fig. 26 e, *Si. V., Sp. V.*). Behind the spiral valve the subintestinal vein tapers off in the region of the anus. The portal system is thus formed by the left lateral vitelline and subintestinal veins and their tributaries that pass into the left side of the liver anteriorly, where they form a vascular channel extending along the left margin of that organ (Text-fig. 26 e, *H. P. V.*). This lateral channel appears with the formation of the portal system, and, passing back along the margin of the liver, breaks up into capillaries in its substance, from which numerous hepatic radicles convey the blood to the posterior vena cava. The development of the subintestinal (portal) vein with its tributary vessel from the spiral fold essentially resembles that of the same two vessels in the elasmobranch (20), except that

in the elasmobranch it is the left half of the venous ring circling the gut, not the right, that disappears.

Sinus Venosus.—The sinus venosus is formed by the junction of the ducts of Cuvier, and comes early to lie on the right of the auricle, opening on the right side of the auriculo-ventricular plug—that is to say, it expands more at the expense of the right than of the left duct of Cuvier, so that the latter remains relatively the longer vessel. With the final development of the liver and the posterior vena cava and the disappearance of the lateral vitelline and subintestinal veins, the sinus venosus becomes drawn out posteriorly and so acquires the irregular pear-shaped formation of the adult chamber. The sinu-auricular aperture and the development of the pulmonary vein and fold and their relations to the sinus have already been described in detail; it will suffice to re-state that the pulmonary vein passes from right to left in the roof of the sinus, and arches down obliquely to the left in a fold across its anterior wall to reach the left auricle. In the adult the sinus venosus is dorsal to the heart, and its ventral, anterior and lateral walls have a covering of pericardium while its dorsal wall is continuous with that structure. The closing of the pericardiac space in front of the liver behind the heart causes a contraction externally dividing the posterior vena cava from the sinus venosus. This contraction is represented in the interior of the sinus by a little projecting ledge. The subintestinal and lateral vitelline veins open into the sinus only for a short period, and the ducts of Cuvier, the posterior vena cava and the coronary vein are the only vessels permanently connected with it.

Inferior Jugular, Subclavian and Lateral Cutaneous Veins.—The inferior jugular veins appear at Stage 31 as little vessels passing ventrally to the branchial arches, backwards along the lateral surfaces of the pericardium, and opening on to the ventral surfaces of the anterior cardinal veins at the outer ends of the ducts of Cuvier (Text-fig. 24 E, *Inf. J.*). These vessels are homologous with those of the same name in the Urodeles. The subclavian veins appear

a little later (Stage 31+), passing inwards from the rudimentary pectoral limbs and entering the anterior part of the pronephric sinuses on their outer sides (Text-fig. 24 *e*, *ScL*). As the pronephric tubules and the outer part of their sinuses atrophy, the subclavian veins come to open into the outer sides of the proximal part of the anterior cardinal veins approximately opposite the entrance to the anterior jugular vessels. In the adult, owing partly to the straightening of the proximal parts of the anterior cardinal veins, which are at first directed laterally, and also partly to the marked elongation of the body in *Lepidosiren*, the inferior jugular and subclavian veins appear to enter comparatively far forwards along the anterior cardinal vessels (Text-fig. 3, *Inf. J.* and *ScL*). At Stage 32 two small lateral cutaneous veins appear one on either side, opening into the subclavian veins from behind (Text-fig. 24 *e*, *Lat. C.*). They pass a little distance backwards in the superficial layers of the body-wall and receive two or three small veins through the body musculature from the vertebral region.

Coronary Vein.—The coronary vein appears on the right outer wall of the ventricle while that surface of the heart is still applied against the sinus venosus posteriorly (Stages 31–32)—that is to say, while the heart loop is still transverse to the axis of the embryo. The little vessel opens from the surface of the ventricle into the sinus, and as the long axis of the ventricle becomes parallel with that of the body, the vein is considerably stretched and carried on to the posterior surface of the ventricle. With the heart in the adult position the coronary vein is on its right dorsal surface, and opens on to the floor of the sinus venosus behind a little fold whose free margin is directed posteriorly.

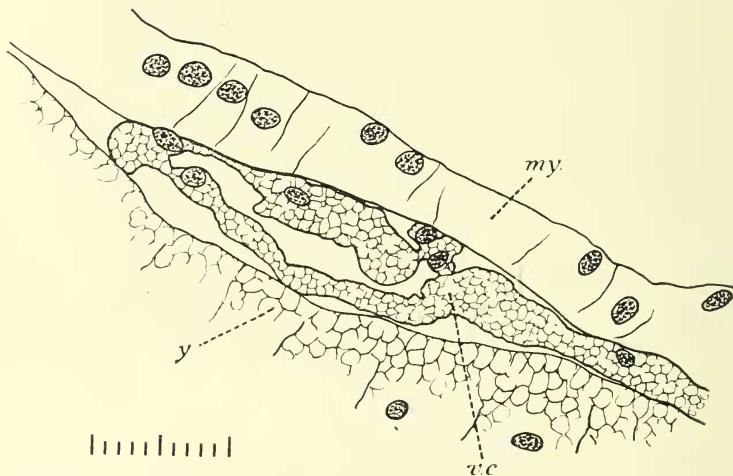
VI. ORIGIN OF VESSEL- AND BLOOD-CELLS.

Vessel-cells.—At Stage 23 the lateral mesoderm is delaminating over the surface of the yolk. The rather columnar cells of the splanchnic mesoderm in the cardiac

region can already be distinguished; the coelomic chinks are just appearing, and, lying between the columnar layer and the endoderm are the comparatively large, flattened, heavily yolked cells, similar to the young mesenchyme cells that later form the rudiments of the vitelline veins.

These vessel-cells, therefore, appear synchronously with the definition from the yolk or endoderm of that part of the splanchnic mesoderm that will, later, constitute the myocardium.

TEXT-FIG. 27.

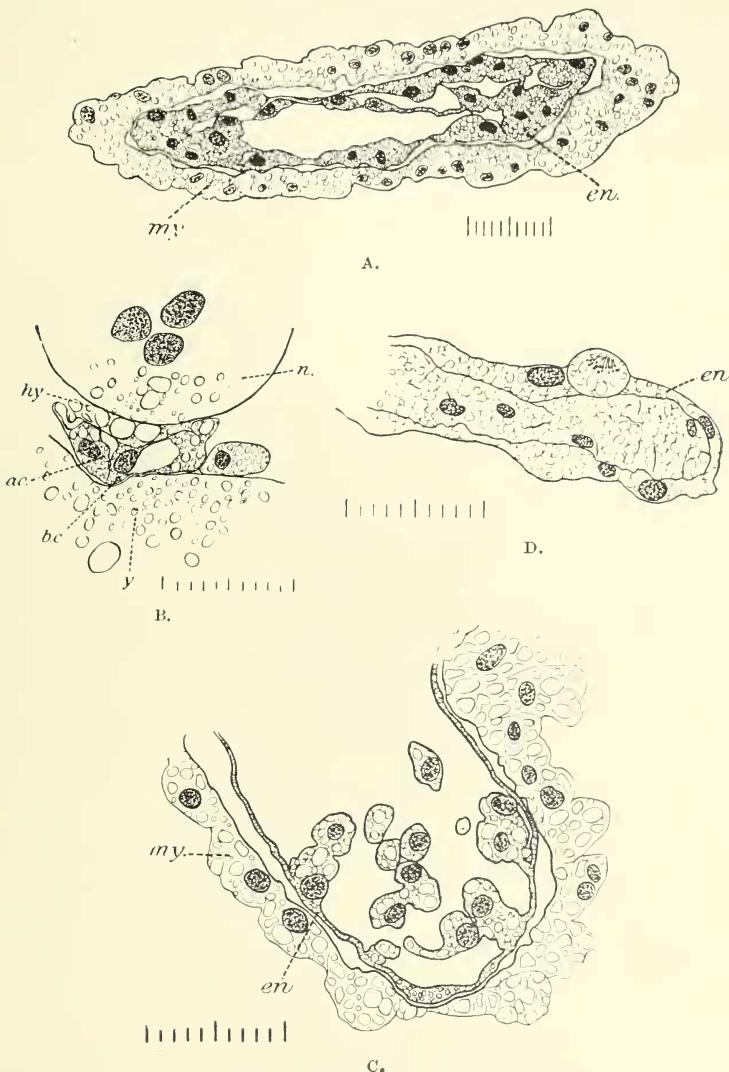


Section showing vacuolation and fusion of adjacent vessel-cells.
my. Myocardiac layer. *v. c.* Vessel-cells. *y.* Yolk.

dium: they are closely wedged between the mesoderm and endoderm, and, posterior to the cardiac area, they merge into the ordinary cells over the yolk. A little later the endothelial vitelline vessels are formed from the vessel-cells between the yolk and the myocardial mesoderm, apparently by a process of intra-cellular vacuolation combined with a syncytial fusion of adjacent cells and the budding off into the lumen of the vessel of free blood-cells from the interlacing branches of the syncytium (Text-fig. 27, *v. c.*).

The endothelial cells of the lateral ventral aortæ are similarly formed, while, once the ventral aortæ extend

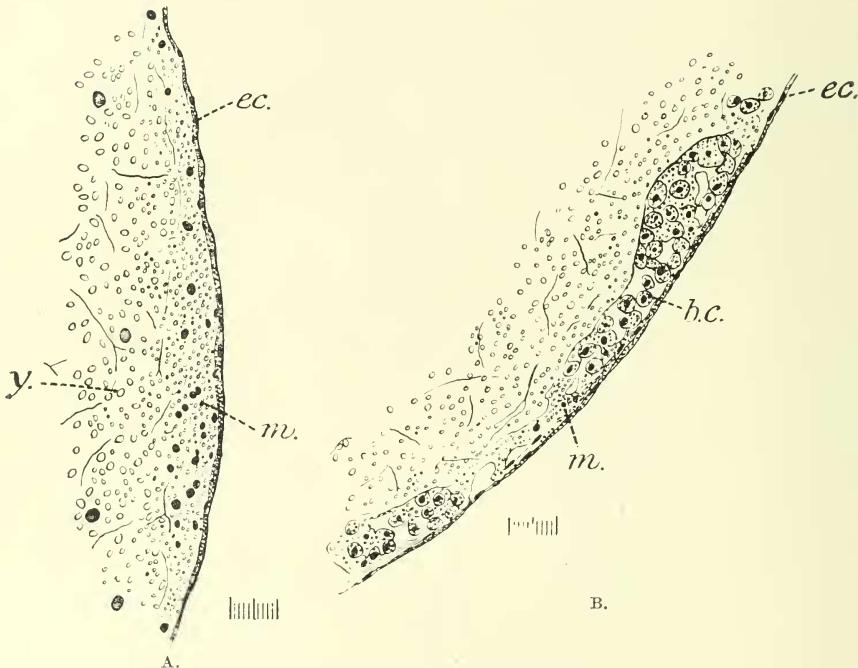
TEXT-FIG. 28.



A. Transverse section through the heart showing syncytial condition of the endocardium and free cells being separated from it. B. Section transverse to aorta at Stage 23 showing vacuolation and fusion of the endothelial cells with corpuscle about to be shed into the lumen of the vessel. C. Sagittal section through heart at Stage 26, showing corpuscle being shed from the endothelium. D. Right sinu-auricular angle. Endothelial cell being shed into lumen of heart. *ao*. Aortic endothelial cells. *b, c*. Corpuscle. *en*. Endocardial syncytium. *en*. Endothelium. *hy*. Hypocardial cells. *my*. Myocardium. *n*. Notochord. *y*. Yolk.

beyond the margins of the endodermic pharyngeal rudiment, their walls are formed directly by the canalisation of the mesenchyme cells of the head region. The posterior cardinal vein and the glomerular arteries are formed from the mesenchyme layer already mentioned as lying between the

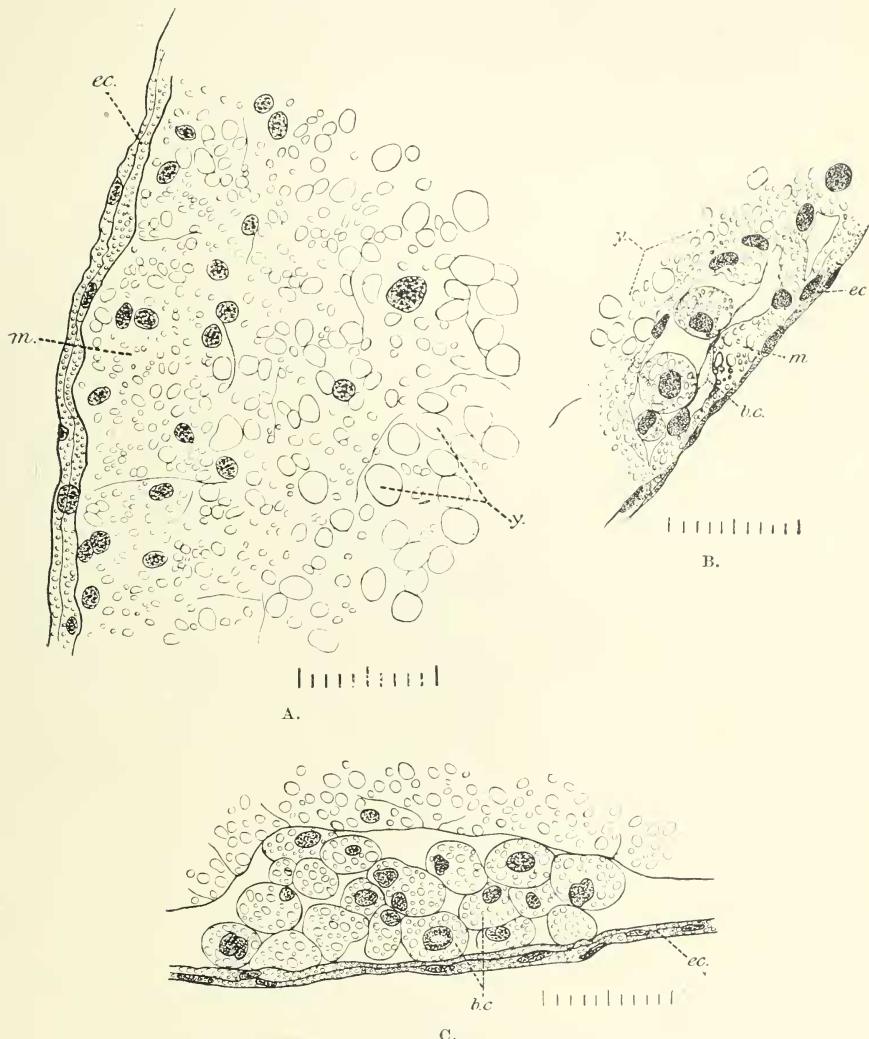
TEXT-FIG. 29.



A. Section at the periphery of the yolk showing the mesoderm layers (characterised by smaller nuclei and finely fragmented yolk-granules), ill-defined from the yolk, which has large scattered nuclei and large granules. B. Section at periphery of the yolk showing the formation of the free blood-corpuscles in the mesoderm layers. *b.c.* Primitive blood-corpuscles. *ec.* Ectoderm. *m.* Mesoderm.

pronephros and the yolk, while the dorsal aorta is formed by sclerotome cells that pass in from either side ventral to the hypocorda (Text-fig. 28 *b*, *ao.*) In all these situations probably the young endothelial cells continue for a time to

TEXT-FIG. 30.



A. High-power drawing of section similar to Text-fig. 29 A.
 B and C. High-power drawings of sections similar to Text-fig. 29 B.
 bc. Primitive blood-corpuscles. ec. Ectoderm. m
 Mesoderm. y. Yolk.

shed free rounded blood-cells into the lumen of the developing vessels. In the smaller vessels the actual shedding is difficult to detect, but the process is evident enough in the heart (Text-fig. 28 *a, c* and *b, en.*)

Blood-cells.—On the surface of the yolk the lateral mesoderm is at first only to be distinguished from the underlying endoderm or yolk-cells by the increased number of somewhat smaller nuclei and the more finely fragmented

TEXT-FIG. 31.

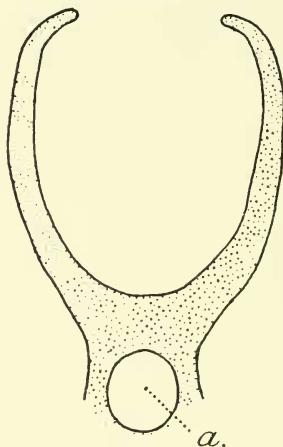


Diagram of a plane surface projection of the cardio-anal bands of multinuclear mesoderm. *a.* anus.

condition of the yolk-granules (Text-fig. 29 *a, m.*) The nuclei are generally arranged in one, but here and there in two or even three irregular layers, while the cell margins are not sharply defined, the appearance being that of multinuclear masses of yolk-laden protoplasm (Text-fig. 30 *a, m.*)

The doubling or trebling of the nuclear layer occurs mostly in little scattered patches over the surface of the yolk, but there is one continuous conspicuous band of two or even three nuclear layers (Text-figs. 29*A* and 30*A, m.*) in thickness on each side along a line extending from the cardiac region backwards and ventrally to the anus, where it merges

in the thicker ventral mesoderm layer. Projected on a plane surface, this multinuclear region of the lateral mesoderm would have somewhat the outline of Text-fig. 31.

The mesoderm layer over the yolk now gives rise by repeated nuclear division to a thin outer layer of splanchnic mesothelium, and internal to this, to free rounded cells—the primitive blood-corpuscles—contained in irregular lacunar spaces formed by the outer walls of the syncytial masses (Text-fig. 30B, *bc.*)

The formation of blood-cells is most active where the mesoderm layer is thickest, and is therefore most noticeable in the scattered areas over the yolk and along the cardio-anal lines already mentioned. In these regions cell-nests of varying sizes are formed, packed with round blood-cells floating in fluid plasma (Text-fig. 30 b and c, *bc.*)

These cell-nests communicate, forming irregular channels, and finally, the vitelline meshwork is established, bringing the whole extent of the vascular mesoderm elements into relation with one another. Anteriorly the vitelline system communicates with the veins along the margins of the yolk and caudally with the aorta and caudal vein.

These observations on the development of the elements of the blood-vascular system in *Lepidosiren* point entirely to their being of mesodermic origin (6).

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DESCRIPTION OF PLATE 5.

Illustrating Dr. J. I. Robertson’s Memoir on the “Development of the Heart and Vascular System of Lepidosiren Paradoxa.”

REFERENCE LETTERS.

A.A. Third, fourth, fifth and sixth, the four persistent aortic arches. *A. S.* Interauricular septum. *A. V. pl.* Auriculo-ventricular plug in auriculo-ventricular opening. *a. b. c.* Three rows of vestigial pocket valves, each row having three valves with traces of smaller irregular valves between them. *B. Ag.* Bulbo-auricular groove. *B. C. d.* Distal segment of bulbus cordis. *B. C. p.* Proximal segment of bulbus cordis. *B. C. t.* Transverse segment of bulbus cordis. *B. R. 3.* Left longitudinal valve in the distal segment of the bulbus cordis. *b.* Dorsal row of vestigial valves in the proximal segment of the bulbus. *C. V.* Cut ends of coronary vein. *D.* Constriction between *B.C.t.* and *B.C.d.* *L. A.* Left auricle. *L.D.C.* Left ductus Cuvieri. *P. B.* pericardiac band. *P.* Constriction between *B. C. t.* and *B. C. p.* *Per.* Pericardium. *P. f.* Pulmonary fold guarding opening of pulmonary vein. *P.V.* Pulmonary vein. *P. V. C.* Entrance of the posterior vena cava to the sinus venosus. *R. A.* Right auricle. *r. D. C.* Right ductus Cuvieri. *r. S. A.* Right sinu-auricular fold; the arrow indicates the sinu-auricular aperture. *S. Ao.* Prominence of the ventral aortic septum, which is formed by the fusion of the left longitudinal and spiral valves in the extremely short ventral aorta. *Sp. V. d.* Distal part of spiral valve. *Sp. V. p.* Proximal part of spiral valve. *Sp. V. t.* Transverse part of the spiral valve. *S. V.* Sinus venosus. *t. f.* Transverse furrows at the base of the spiral valve showing traces of valvular pocketings. *V.* Ventriele. *V. B. o.* Bulbo-ventricular orifice indicated by arrow-head. *V. S.* Interventricular septum.

Fig. 1.—Drawing of the adult heart from the right side magnified about $3\frac{1}{2}$ times. The right walls of the right auricle and ventricle and of the proximal part of the bulbus cordis have been removed to show

the internal structures. The sinu-auricular aperture is indicated by an arrow that is seen against the pulmonary fold.

Fig. 2.—Drawing of the heart from the left side, magnified about $3\frac{1}{2}$ times. The left walls of the left auricle, ventricle and bulbus cordis have been removed. The opening of the pulmonary vein (*P.V.*) into the left auricle is indicated by an arrow, as is also that of the bulbus from the ventricle (*V. B. o.*).

Fig. 3.—Drawing of the proximal segment of the bulbus cordis, magnified about 5 times. The dorsal wall has been cut open a little to the right of the middle line, so that the dorsal row of vestigial valves has been divided unequally. No part of the bulbus wall has been removed.

Fig. 4.—Drawing of the bulbus cordis from the ventricular side magnified about $3\frac{1}{2}$ times. The ventral wall of the bulbus has been removed in the distal and transverse segment.

Fig. 5.—Drawing of the heart (magnified about 50 times) about Stage 31. The transverse position of the heart is still distinct.

Fig. 6.—Drawing of heart (magnified about 50 times) about Stage 33. Owing to the various growth adjustments the transverse position of the heart is rapidly being lost.

Fig. 7.—Drawing of heart (magnified about 50 times) about Stage 35. The position of the heart is now practically that of the adult condition.